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Volume 33. No. 2 April, 1958

THE JOURNAL OF HORTICULTURAL SCIENCE

(Formerly The Journal of Pomology and Horticultural Science)

Subscription Rates:
SINGLE NUMBERS 20/- EACH
ONE VOLUME (FOUR NUMBERS) 60/- (RATE FOR CANADA & U.S.A., $8.50) POST FREE

PUBLISHED BY
HEADLEY BROTHERS LTD
109 Kingsway London WC2 England

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COMMONWEALTH MYCOLOGICAL
23 MAY 1958

THE JOURNAL OF HORTICULTURAL SCIENCE

The Journal is an official organ of the Horticultural and Agricultural Research Station, Long Ashton, Bristol, and the Horticultural Research Station, East Malling, Kent. The Publication Committee welcome papers of horticultural interest from all other sources.

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T. WALLACE

An Appreciation

PROFESSOR WALLACE's name first appeared in the *Journal of Pomology and Horticultural Science* in June, 1925, when the forerunner of a long series of papers describing the results of experiments on the manuring of fruit trees was published. During the years that followed until 1946, twenty-two papers appeared under his name, which have laid the foundations of our present-day knowledge of the nutrition of horticultural crops.

In 1943 he succeeded Barker as Director of Long Ashton and as Joint Editor of the *Journal*. In spite of his heavy commitments as Director of the Research Station, he did not take his duties to the *Journal* lightly and has personally read and commented on nearly all the papers submitted, of which 295 have been published in the twelve volumes from 1945-57. Time for this exacting work was found sometimes during train journeys and sometimes by reading far into the night. Nevertheless, he always managed to bring to each paper the full benefit of his clear mind ; those who follow him will long miss his wise and kindly judgment.

After the first two volumes this *Journal* was primarily the responsibility of the fruit research stations, and in the early years most of its contents were mainly of interest to those concerned with fruit but, in the second ten volumes, it was evident that the field of horticultural interest was widening. This tendency was encouraged by Wallace and, in 1947, the title became the *Journal of Horticultural Science*. From then on, the Publication Committee was enlarged and, by the end of his term of office, included the Directors, or their representatives, of most of the important centres of horticultural research in the United Kingdom.

During his term as Editor, he has consistently maintained that the function of the *Journal* was to provide a means of presenting the results of experimental work of scientific importance and of interest to horticulturists. Unsupported by any special scientific society and of limited interest to the ordinary grower, the *Journal* could hardly be expected to attain a high circulation. Nevertheless, only once has it sought outside financial assistance and the list of subscribers all over the world has steadily grown.

Much of this progress must be attributed to Wallace's insistence on the high quality of the contents. Aided by two very efficient Assistant Editors, first W. M. Ware and then W. Brown, and by a band of specialists, among whom R. H. Stoughton has been outstanding for several years, he has insisted on clear and succinct presentation and steadily set his face against the acceptance of slipshod reports or papers describing work of inferior quality. The publication of long reports, embellished with much undigested tabular matter, is no longer financially possible ; but apart from such a consideration, his insistence on clarity and conciseness has resulted in an immeasurable improvement in the quality of the papers, for which authors and readers alike will be everlastingly grateful to him.

This is not the place to enlarge upon Wallace's contributions to horticulture as a

whole, not only as Director of Long Ashton, but in many other capacities, all of which have brought him many well deserved honours and have been acknowledged by others in recent months. Nevertheless, it should be emphasized that the knowledge and experience that he has gained through his many contacts have been of the utmost value to the *Journal*—that he has found the time to give of them so unstintingly can only be attributed to an apparently unlimited capacity for hard work.

The *Journal* has now the support of a long list of Associate Editors, many of whom have rendered services of conspicuous value in the past. It is a pleasure to inform subscribers that Wallace has consented to join that distinguished band. Although, therefore, we can no longer look to him for the advice and guidance he has unfailingly given for so many years, his services to the *Journal* will by no means be wholly lost.

T.N.H.

ROOT STUDIES

XII. ROOT SYSTEMS OF APPLE ON MALLING ROOTSTOCKS ON FIVE SOIL SERIES*

By E. G. COKER†

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It was shown by Hatton (1926) that the general principles of rootstock effect in apples held good on different soils, but that each soil had a characteristic effect on the performance of different rootstocks. Studies by Rogers and Vyvyan (1934) on the root systems of apples on loam, sand and clay soils showed large differences in root growth on the different soils.

In 1935–6 and 1937–8, sets of trees on a series of Malling rootstocks were planted on five contrasting soil series in Kent. The behaviour of these trees up to ten years of age has been described by Rogers (1946). On each plot some trees were set aside for root excavations ; these were begun during October 1951 and continued during successive winters until February 1955.

It was decided to study trees of Cox's Orange Pippin on Malling Nos. I, II and IX, i.e. on two vigorous rootstocks whose relative performance varied on different soils, and on a dwarfing one. Trees whose growth was typical of each rootstock-scion combination were selected for excavation.

Methods.

On all plots the " combined " method of root excavation described by Rogers and Vyvyan (1934) was used. The roots were cut out in half-metre squares in successive sections, in layers from 0–30 cm., 30–100 cm., and below 100 cm. in depth, labelled, weighed, and subsequently reconstructed with the aid of a gridded root plan on which the depth and position of the roots were indicated. In the first excavation, on plot A, the entire root systems of the three selected trees (one on each rootstock) were excavated. To save labour and to restrict costs, only one 90° sector from each of the three selected root systems was excavated on the remaining four plots. Root plans were made. Roots were weighed in relation to depth (0–30 cm., 30–100 cm., and deeper than 100 cm.) and distance from the tree (within the metre square round the tree, outside the three metre square round the tree, and between these. On plots B to E measurements were also made of the length of roots thicker than 1 mm. in diameter. Roots were brought back to the laboratory in batches from the 3 depths and from different areas of the root system, and a length of string was laid in turn along each branch root thicker than 1 mm. The length corresponding to each group of roots was measured. The point at which a root became thinner than 1 mm. was found by using a metal gauge. Root systems were reconstructed and photographed.

* Based on a thesis approved for the degree of Master of Science in the University of London.

† Now at the Hertfordshire Institute of Agriculture, St. Albans.

Soil profiles.

The soil series, classified by Lee (1931) and Furneaux (1932), were : A, Wye Series (brick earth) ; B, Rattle Series (clay-with-flints) ; C, Lamberhurst Series (Wadhurst clay) ; D, Curtisden Series (Tunbridge Wells sand) ; E, Ladham Series (brick earth of the High Weald). Profile descriptions of the plot sites, to 3 feet in depth, have been given by Rogers (1946). Additional relevant details are summarized below.

A. Wye Series. The soil, mainly a very fine sandy loam, extended to the chalk at 170–230 cm. in depth. Below 160 cm. the soil became heavier, passing into sandy clay-with-flints. Above and in contact with the chalk was a layer of chocolate-brown clay loam analogous to the " pug " reported over ragstone by Rogers and Vyvyan (1928). Drainage was very good.

B. Rattle Series. The profile on the site was a transitional type between the Rattle and the Selstead Series (Lee, 1931). It consisted of clay-with-flints reworked over brick earth (" plateau loam " of Lee, 1931), which varied from a few to 120 cm. in thickness, and this in turn overlaid clay-with-flints which extended to the chalk at 150 cm. or deeper. As on plot A, a layer of chocolate-brown clay loam of good crumb structure was present immediately above the chalk. Drainage was good.

C. Lamberhurst Series. The profile on this site was poorly drained. On this clay soil, drainage was satisfactory to about 70 cm., where a tile drain was found, but was impeded below this depth.

D. Curtisden Series. This was a sedentary soil. The very fine sand became more compact with increasing depth and showed symptoms of defective drainage below 55 cm. At 80–95 cm. the sand was cemented into an almost continuous layer of ironstone 25 cm. thick. This was probably the " B " horizon of a podsol profile.

E. Ladham Series. The profile consisted of brick earth 80–90 cm. in depth, over what was probably a truncated sedentary profile of Tunbridge Wells sand. Coarse sand extended below the brick earth to 95–110 cm. in depth where there was a continuous layer of ironstone (probably " B " horizon material) about 20 cm. thick.

Results.

Distribution of roots in relation to soil characters.

A. Wye Series. Although the soil was deep and well drained, the main scaffold roots of all three rootstocks had developed horizontally between 15 and 40 cm. in depth. This part of the profile was very favourable to root growth, for fibrous roots grew more densely in this region than elsewhere. Below this, to about 120 cm. deep, the soil was freely exploited by roots of all three rootstocks. Below 120 cm. deep the roots of M.II, and to a lesser extent M.IX, branched and spread widely, especially in the clay loam above the chalk. Only a few roots of M.I penetrated deeply and they failed to spread widely or branch freely at this depth (Table I and Fig. 1). Fine roots grew freely in soil filling cracks in the chalk, but they failed to penetrate the chalk itself more than about 1 cm.

B. Rattle Series. As on plot A, the main scaffold roots of M.I and M.IX spread horizontally between 20 and 40 cm. deep, though those of M.II were deeper. Roots which reached the chocolate-brown clay above the chalk grew more freely in it than in the soil above (Fig. 2). Roots of M.II grew freely in soil more than 250 cm. in depth, but roots of M.I were mainly less than 120 cm. deep, though some penetrated

more deeply. M.IX was similar to M.I (Tables I and II). On all rootstocks, root development, especially in the shallower layers, was much less dense than on plot A, and some patches within the soil block were not exploited by roots.

C. Lamberhurst Series. With all three rootstocks, most main roots were found between 20 and 50 cm. deep, being deeper than on plot A, although poor soil aeration and a rising water table (indicated by iron concretions and grey mottling) largely restricted root growth to the top 70–80 cm. of soil. Many roots were killed back but had grown out above this level and a few had penetrated deeply (Tables I and II, Fig. 3).

D. Curtisden Series. With all three rootstocks, fibrous roots grew densely in the soil less than 30 cm. deep and most roots were found within 55 cm. of the soil surface. Roots which grew below this depth in the poorly drained compact sand branched weakly and penetration in depth was almost entirely restricted to the soil above the ironstone " pan " at 80–95 cm. (Tables I and II, Fig. 4).

E. Ladham Series. The main scaffold roots of all rootstocks were found between 30 and 70 cm. deep, being deeper than on other soils, though the ironstone " pan " at 95–110 cm. restricted penetration in depth. Although some deep roots had been killed back where lateral water seepage was taking place through the subsoil, these had, in contrast with those on plot D, branched freely into the loose subsoil from above the killed portion (Tables I and II, Fig. 5).

TABLE I.

Root weight at different depths.

Plot	Rootstock	Percentage weight at :		
		0–30 cm.	30–100 cm.	100 cm.+
A	I	76·1	20·5	3·4
	II	62·9	27·7	9·4
	IX	79·5	13·6	6·9
	Mean	*72·8*	*20·6*	*6·6*
B	I	69·5	23·0	7·5
	II	37·6	33·1	29·3
	IX	77·3	22·7	0·0
	Mean	*61·5*	*26·3*	*12·2*
C	I	43·0	57·0	0·0
	II	43·3	56·0	0·7
	IX	27·5	71·0	1·5
	Mean	*37·9*	*61·4*	*0·7*
D	I	54·0	45·2	0·8
	II	57·6	42·0	0·4
	IX	74·5	25·5	0·0
	Mean	*62·0*	*37·6*	*0·4*
E	I	35·0	64·2	0·8
	II	29·1	69·6	1·3
	IX*	—	—	—
	Mean†	*32·1*	*66·9*	*1·0*

* Trunk pulled out in 1951. † I and II only.

Weight and length of roots.

Table I gives the distribution by weight of ungraded roots at different depths. To a large extent this indicates the distribution of the main scaffold roots, for a few thick roots outweigh a mass of thin ones of far greater length. Table II gives the distribution, in terms of length, of roots thicker than 1 mm. for plots B, C, D and E. By placing greater emphasis on small roots the latter data provide a more sensitive measure of root distribution than do the ungraded weights. In both Tables, figures for plots B–E are based on a 90° sector of each root system.

TABLE II.

Length of roots thicker than 1 mm. at different depths.

Plot	Root-stock	Total root length (m.) in 90° sector of root system	Mean length (cm.) per sq. m. root area	Percentage length at :		
				0–30 cm.	30–100 cm.	100 cm. or more
B	I	350·6	2,627	45·2	44·4	10·7
	II	282·0	3,576	18·2	55·4	26·4
	IX	48·5	3,644	45·0	42·3	12·7
	Mean		*3,297*	*36·1*	*47·3*	*16·6*
C	I	435·5	3,960	42·2	55·5	2·3
	II	221·5	3,656	37·3	61·2	1·5
	IX	158·2	4,312	31·0	64·7	4·3
	Mean		*3,909*	*36·8*	*60·4*	*2·7*
D	I	432·2	5,660	57·3	41·2	1·5
	II	295·8	4,932	56·0	43·3	0·7
	IX	160·5	3,208	56·4	43·6	0·0
	Mean		*4,600*	*56·6*	*42·7*	*0·7*
E	I	525·0	4,200	51·0	47·3	1·7
	II	271·2	2,856	40·5	54·0	5·5
	IX	—	—	—	—	—
	*Mean**		*3,528*	*45·8*	*50·6*	*3·6*

* I and II only.

Area of rooting and linear spread of roots and branches.

An estimate of the area of soil penetrated by the lateral spread of each root system was obtained by counting the number of half-metre squares on the gridded field plans containing roots of each root system or part of a root system (Table III). Some squares contained roots from two or more trees. Table IV gives data of root spread and branch spread under the various conditions. As in Tables I and II, the figures for plots B–E were based on data from a 90° sector of each root system.

Relation between adjacent root systems.

On plot A the roots of trees on M.IX branched sparsely and roots of adjacent trees on this rootstock interlaced freely. By contrast, M.II formed a closely branched root system which did not interlace freely with roots of adjacent trees on M.I or M.IX. There were more deep roots on M.IX where they had grown towards the

Table III.

Area (sq. m.) of root systems.

Plot	M.I	M.II	M.IX	Mean per plot
A	46·0	34·0	8·0	29·3
B	37·5	31·5	7·5	25·5
C	44·0	24·3	14·7	27·6
D	30·5*	24·0*	20·0	24·8
E	50·0	38·0	14·0†	34·0
Mean per rootstock	41·3	30·4	12·8	

* Root-pruned in 1948–9 by mole draining down middle of row.
† Trunk pulled out in 1951 ; main roots still intact in February, 1955.

Table IV.

Branch and root spread (m.);
mean of two measurements, one along and one across the tree row.

Plot	Root-stock	Mean root spread	Mean branch spread	Ratio of root spread to branch spread	Mean ratio
A	I	11·5	5·87	1·96	
	II	7·55	6·50	1·16	
	IX	4·30	2·75	1·57	1·53
B	I	8·70	3·50	2·49	
	II	7·50	5·50	1·36	
	IX	3·20	1·65	1·94	1·93
C	I	7·90	6·25	1·34	
	II	6·50	5·85	1·04	
	IX	4·90	3·30	1·48	1·29
D	I	6·70*	5·2	1·29	
	II	5·50*	4·9	1·12	
	IX	4·8	3·3	1·46	1·29
E	I	8·60	7·15	1·22	
	II	7·80	6·20	1·26	
	IX	4·50†	—	—	1·24
Mean value	I			1·77	
	II			1·17	
	IX			1·61	

* Root-pruned 1948–9 by mole draining down middle of row.
† Trunk pulled out in 1951 ; main roots still intact in February, 1955.

vigorous M.II than where they had grown towards another M.IX. Near the adjacent M.IX competition was less intense and lateral roots extended farther.

Detailed observations were not made on the other plots where the root systems had been only partially uncovered. An assessment of the extent of root interlacing is given in Table V and, as is to be expected, this is directly related to the area of spread of rooting on each plot.

TABLE V.

Percentage root area in half-metre squares containing roots of more than one tree.

Plot	Mean root area (sq. m.)	Percentage of root area in which roots interlaced
A	29·3	27·1
B	25·5	11·7
C	27·6	18·3
D	24·8	17·0
E	34·0	28·0

DISCUSSION.

The discussion falls naturally into two main parts : the effects on root development of (*a*) soil conditions, and (*b*) rootstock variety. The effects of soil conditions on the root development of apple have already been described by many authors, so that this part of the discussion will be limited mainly to features of special interest in this study.

EFFECTS OF SOIL CONDITIONS.

Depth, drainage and compaction.

In many respects the root distribution in depth found on plots A and B was similar and contrasted with that found on plots C, D and E. These two groups differed in respect of soil depth and quality of the underlying drainage.

Plots A and B were clean cultivated. On both, the underlying chalk, at depths up to 250 cm., limited depth of root penetration. There was free drainage into the chalk and roots grew freely in fissures filled with soil but failed to penetrate the chalk itself. On both plots, with one exception, scaffold roots extended more or less horizontally near the surface though many laterals penetrated deeply. The distribution in depth of roots on B (clay-with-flints) was comparable with that found on A and other sandy and loamy soils, rather than with the clay with impeded drainage on plot C and with that described by Rogers and Vyvyan (1934). This confirms the observation of Boynton (1938) that where, on a clay soil, the internal and underlying conditions of water drainage are satisfactory, roots will penetrate deeply.

Plots C, D and E were on shallower soils over the Hastings Beds and were in grass. On these plots the downward movement of water was impeded (by heavy clay on C and by an ironstone pan on D and E), and surplus water moved laterally in the subsoil down the slope to the ditches. This was facilitated by tile and mole drains on C and D. On all these plots the main scaffold roots were deeper than on plots A and B, though the full depth of root penetration was less (Figs. 1–5).

PLATE I

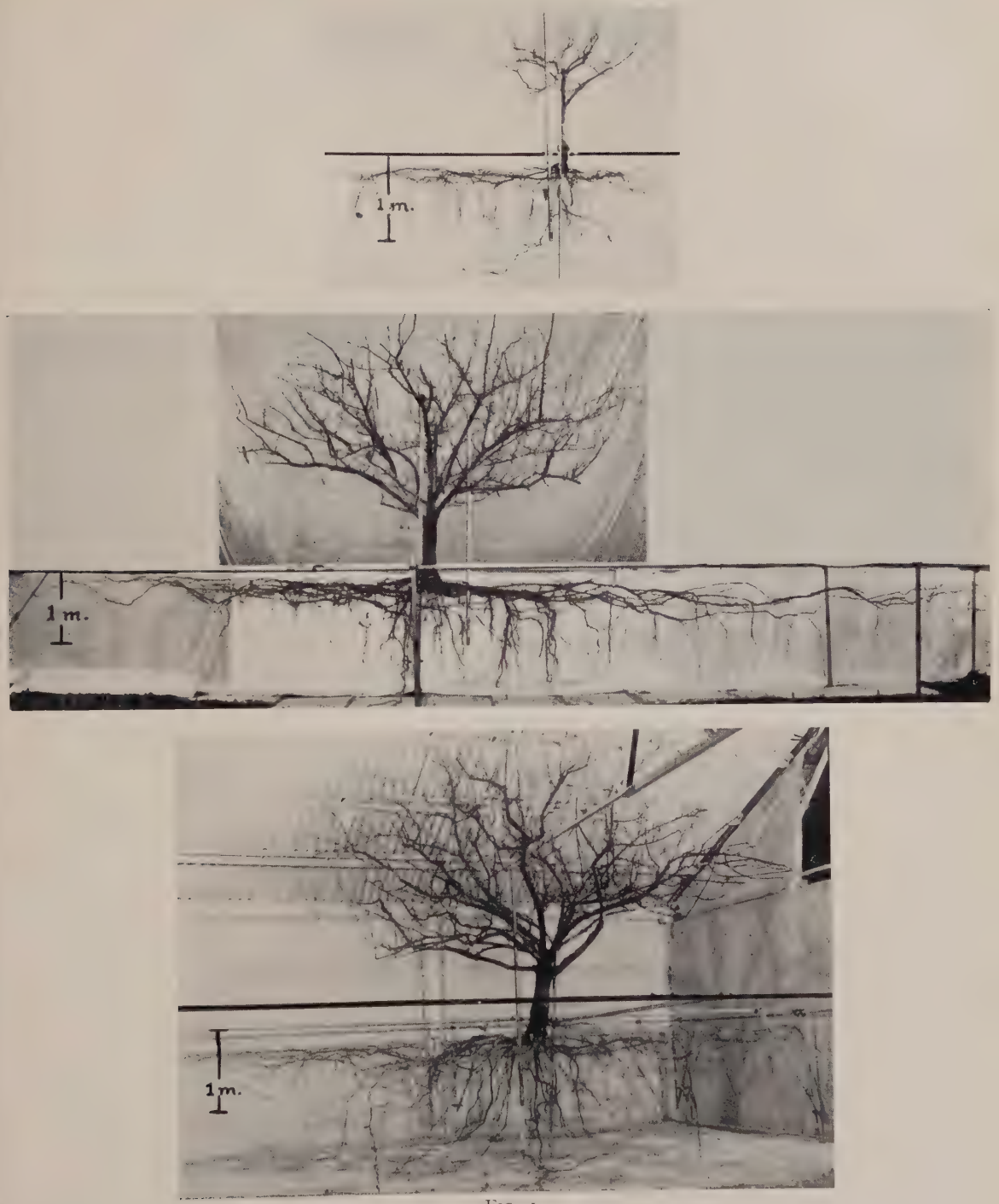

Fig. 1.

Root Systems of Cox's Orange Pippin on three rootstocks from plot A (Wye Series), excavated at 16 years old.

Top: on M.IX. Vigorous main root system fairly near surface, many roots penetrating deeply.

Middle: on M.I. Vigorous main root system near surface, spreading widely in relation to branches; some deep roots present.

Bottom: on M.II. Vigorous main root system near surface and many roots deeper than 100 cm.

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FIG. 2.
90° sector of root system of Cox's Orange Pippin on M.II from plot B (Rattle Series), excavated at 18 years old. Note large number of roots below 100 cm. deep.

FIG. 3.
As in Fig. 2, but from plot C (Lamberhurst Series). Note wide spread of branches in relation to roots, and the killing back of roots.

FIG. 4.

90° sector of root system of Cox's Orange Pippin on M.IX from plot D (Curtisden Series), excavated at 19 years old. Note wide spread of branches in relation to roots and limitation of depth of rooting at 80-95 cm. (because of soil compactness and impeded drainage).

FIG. 5.

Main part of a 90° sector of root system of Cox's Orange Pippin on M.I from plot E (Ladham Series), excavated at 17 years old; photographed *in situ*. Note relatively deep position of main roots and restriction of depth of rooting by an iron pan at 1-1¼ metres.

The pattern of root development on plot C was similar to that described by Rogers (1932) on a clay soil with impeded drainage, being in general limited to the depth of the tile drains.

On both plots D and E the depth of root penetration was limited by an ironstone pan to 90–100 cm. On D, a sedentary soil, the subsoil below about 55 cm. was compact and showed patches of defective drainage ; although roots penetrated to the " pan " they did not branch freely below 55–60 cm. and the deeper portion of the soil was poorly exploited. By contrast, plot E was on drift soil, the deeper part of the profile being loose in structure, and water moved through it without artificial drainage. Roots branched freely in this layer as well as in the shallower soil. Thus the depth of soil densely exploited was greater on E than on D, though the depth of maximum penetration was similar.

Despite textural differences between plots C, D and E, the depths of formation of the scaffold roots were similar and contrasted with those on plots A and B. The observation of Rogers and Vyvyan (1934), that the main scaffold roots were situated more deeply on a heavy clay than on a loam or sand, does not conflict with these results. In their studies the loam and sand were freely drained but the clay soil was not. This difference in depth of scaffold roots probably indicates a distinction between well drained and impeded-drainage soils in the location of the soil zone most favourable to root growth. The main scaffold roots are those early formed roots which have spread and branched more extensively and thickened more rapidly than others. The clear distinction in this respect between freely drained and impeded-drainage soils suggests an association with soil moisture relationships, but it is not yet possible to confirm this. In this connection, besides producing root systems resembling in form those found on a heavy clay by Rogers and Vyvyan (1934), the soils on plots C, D and E produced trees with a smaller root spread in relation to branch spread than on plots A and B.

Effects of soil texture.

Soil texture was less important than drainage and soil depth in the development of the root systems studied, but two effects are worth noting.

A sandy loam top soil appeared to favour a denser root branching in the shallow layers than did a clay loam. On plot A, with sandy loam top soil, a dense layer of fibrous roots was present in the same zone, less than 40 cm. deep (Fig. 1), as were the scaffold roots. On B, with clay loam topsoil, fibrous roots did not branch densely in this layer. A similar contrast was seen between D and C, with sandy loam and clay loam top soil respectively (Table II). On plot B patches within the main soil block exploited by the trees contained no roots, although they did not appear to differ from the rest of the soil. A similar observation was made by Furr and Taylor (1939) who found patches of unexploited soil within the root systems of lemon trees grown on a clay loam, whereas comparable trees on a sandy loam exploited the soil profile uniformly.

On plots A and B the chocolate-brown clay loam found at the junction of the soil with the chalk appeared similar to that described by Rogers and Vyvyan (1934) on the Malling loam over ragstone, another free-draining calcareous rock. This layer of soil appeared very favourable to root growth for, wherever roots reached it, they branched more freely in it than in the soil immediately above. Compared with the layer immediately above it, on plot B this layer showed better crumb structure ;

on plot A, higher levels of available K and Mg ; and on the Malling loam, a higher moisture-holding capacity (Rogers and Vyvyan, 1934).

Effects of rootstock variety.

Depth of soil exploitation.

On all plots some roots from each rootstock penetrated to the full depth of the soil profile. On each of plots C, D and E the depth of root penetration of the three rootstocks was restricted by the same limiting factors to a similar depth, viz. 70–100 cm. Although there was a tendency for M.I to be more shallow-rooted on C and E, the differences in depth distribution between rootstocks on these three soils were not great. On A and B, however, M.II rooted more densely than M.I below about 120 cm. in depth (Table II and Fig. 1). M.IX was intermediate in this respect, being similar to M.II on A and to M.I on B. Thus, differences in the ability of these three rootstocks to exploit deeper layers were shown most clearly where the soil was considerably more than 100 cm. (40 in.) in depth.

Area of root spread.

The largest and most consistent differences between rootstocks were in area of root spread (Table III). It was smallest for M.IX, largest for M.I, while M.II was intermediate. This order of size is the same as that of initial vigour of trees on these rootstocks (Hatton, 1926) and of the relative size of the excavated trees on plots C, D and E. The spread of the branches on M.II was larger in relation to that of the roots than on M.I, but on these excavated trees this did not alter the relation between the order of root spread and tree size already noted. On each of these three plots the depth of root penetration of all the rootstocks was similarly limited, so that the volume of soil accessible to the roots was directly related to the area of root spread.

On plots A and B, trees on M.II were more vigorous than on M.I and it is likely that the smaller root spread was more than compensated for by the better exploitation of the deeper layers already referred to. On these plots the area of root spread and size of trees on M.IX were both more than 50 per cent. less than for comparable trees on plots C, D and E. It was only with M.IX that such large and consistent differences were found and this appears to be a rootstock/soil reaction not yet explained.

SUMMARY.

1. The root systems of fifteen mature apple trees of Cox's Orange Pippin on Malling Nos. I, II and IX rootstocks, planted on five soil series in Kent, were excavated either whole or in part.

2. The five soil series fell into two groups in respect of depth, drainage, and soil management. These were : plots A and B, deep, freely draining profiles over the chalk, and plots C, D and E (under grass), less deep, with an impedance to drainage in the underlying layers.

3. On A and B, root development was similar to that already described for freely drained loamy soils and extended to the underlying chalk. On A, rooting was similar to that found on the Malling loam; on B, root distribution in depth was similar to, though much less dense than, that on A.

4. The soil on C, D and E was of differing texture but rooting was similar in many respects to that for heavy soils with impeded drainage. On D, soil compaction restricted root development.

5. The depth of formation of the main scaffold roots is discussed in relation to the two groups of soils.

6. Trees on M.I on plots C, D and E over the Hastings Beds had a wider branch spread in relation to root spread than on plots A or B over the chalk. The ratio of branch spread to root spread was higher for M.II than for M.I or M.IX on all plots except E, where there was little difference.

7. On all plots, trees on M.I had a substantially greater area of root spread than trees on M.II or M.IX.

8. On A and B, more roots of M.II than of M.I were found deeper than one metre. On C, D and E, depth of root penetration of all rootstocks was limited and there were no large differences between rootstocks in depth distribution of roots.

9. It was concluded that the larger size of trees on M.II than on M.I, on plots A and B, was related to the greater amount of deep roots formed by M.II.

10. Trees on M.IX from A and B were much smaller in root spread and tree size than those from C, D and E, although they were deeper rooting on the former.

ACKNOWLEDGMENTS.

I wish to express my thanks to Dr. W. S. Rogers for his interest and supervision throughout the work. Thanks are also due to Mr. J. E. Goode for much valued assistance in describing the soils and to Mr. E. Y. Jones for taking the photographs. I am also indebted to Dr. T. H. Rose, N.A.A.S., Wye Sub-Centre, for soil analyses.

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(*Received* 21/2/57.)

THE UPTAKE AND DISTRIBUTION OF RADIOACTIVE PHOSPHORUS(^{32}P) IN RELATION TO THE MUTATION RATE IN PLANTS

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THE mutagenic efficiency of radioactive phosphorus, ^{32}P, when measured either in terms of chromosome breakage or of genetic mutation, is now well established (Thompson *et al.*, 1950 ; Bateman and Sinclair, 1950). The relative ease and safety with which the isotope can be used, together with the special rôle of phosphorus in the metabolism of the nucleus, make it particularly suitable for general application in mutation studies. In spite of the relatively high maximum energy of the particle emissions which characterize ^{32}P, their power of penetration is weak when compared with γ or X irradiation. This necessitates the introduction of the isotope into the tissues, which in turn raises problems of distribution and relative concentration in different regions of the plant.

The possibilities of producing economically-valuable variation by increasing the mutation rate in different classes of crop plants have been assessed with varying degrees of optimism by several workers (Granhall, 1954 ; Singleton, 1955). The results so far achieved are too meagre to allow non-speculative comment, and therefore it is proposed in this work merely to present factual data on the uptake, transport and concentration of the mutagen in woody and herbaceous plants.

Previous reports by Stanton and Sinclair (1953) and Ehrenberg and Granhall (1952) have established a number of points in relation to the uptake of ^{32}P by plum and apple trees. The main findings from these investigations were : (1) that uptake through roots or cut ends of dormant branches is slow and results in very low concentration of the isotope ; (2) that injection into stems or branches results in the rapid transport of the phosphorus which becomes concentrated in the meristematic regions ; (3) that, when equivalent doses are compared, ^{32}P effects far less tissue damage and gross morphological abnormalities than X-ray. The experiments described below elaborate and extend these conclusions.

MATERIALS AND TECHNIQUES.

Materials.

The experiments were conducted on apple and pear trees established in pots and on flowering plants of foxglove, tomato and sweet pea. The phosphorus isotope was administered as sodium dihydrogen phosphate treated in the atomic pile at Harwell, and specific activities ranging from 3–36 millicuries per gram (mc/gm.) P were used. Dilutions of a stock solution of near saturation strength provided the desired variations in the administered dose. All treatments were carried out in duplicate.

It is known that between 40 and 50 per cent. of pile-irradiated phosphate is converted into phosphite, but since the major part of these investigations was

conducted on injected material which was therefore not subject to problems connected with differential absorption, the presence of a mixture of phosphite and phosphate is not considered important.

Root uptake method.

Trees were established in silver sand during the dormant season and, before the commencement of active bud break, a complete nutrient solution of low phosphate status (<10 p.p.m.) was applied at regular intervals. Prior to the application of radioactive solution, the pots were thoroughly leached with rain water to remove as much as possible of the free phosphorus from the sand. Varying quantities of phosphate solution containing 80μc/ml. of ^{32}P were applied on 5th May 1955 at a stage when new growth was active and when 1–2 inches of elongation had occurred at the growing points. The plants were afterwards supplied only with rain water until recordings were terminated.

Injection method.

All experiments on injection methods were on plants grown in soil.

Woody species. Holes of 0·75 cm. diameter were drilled into the trunk or branch and midway into the wood. Glass tubing was inserted into the bore hole and secured with grafting wax. The remainder of the procedure can be appreciated from Fig. 1. For safety in handling and introducing the radioactive substance, a hole was drilled near the bottom of the glass bottle through which the solution could be pipetted, or poured through a funnel. Approximately 100 ml. of solution of known strength was administered in this way. The solution was completely absorbed in the course of 12–36 hours, depending on the size of the tree and on the transpiration rate. Further quantities of distilled water were applied for a period of 4 days after injection in order to ensure complete uptake of the dose.

Herbaceous species. The method successfully employed for direct uptake by herbaceous plants consisted of administration through cut ends of the petiole at a distance of 1 in. from the main stem. Thin tangential sections were removed on all sides of the remaining basal part of the petiole and a piece of glass tubing 2 in. long by 1 cm. diameter was secured over the cut end by means of grafting wax. A perfectly water-tight seal was obtained by this method. The radioactive solution was introduced by means of a hypodermic syringe through the open end of the tube, which was afterwards completely sealed. Small amounts, up to 2 ml. of solution of the required specific activity, were administered in this way, and total uptake was completed in 12–24 hours.

Radioactive assay.

All assays were performed on digested samples in an M6 liquid counter, using an EKCO N529 scaler with probe unit. The efficiency of the counter was calibrated against a solution of known activity, and on the basis of these determinations all transformations were based on 3300 counts/sec.=1μc±0·016. The majority of determinations were made on duplicate samples and their mean activity is presented. As most of the comparisons discussed represent clear-cut differences or trends, the sample variances have been omitted. Samples were oven dried, ground, and a small quantity (1 gm.) was digested in 5 ml. of concentrated sulphuric acid with catalyst

in a microkjeldahl flask. Where necessary, dilutions were carried out on the digest to reduce the counting rate to below 200/sec. Except where otherwise stated the activity per gram of dry weight was transformed to the date of sampling on the basis of the decay rate of ^{32}P which has a half-life of 14·3 days.

EXPERIMENTAL RESULTS.

Uptake and transport in woody species.

Comparison of root uptake and injection.

Since similar results were obtained with apple and pear trees no distinction will be made between the two species in the presentation and discussion of results.

Direct comparison between the rate of uptake by roots and that resulting from injection where equivalent doses have been administered is impossible because of the many uncontrollable factors that operate on root absorption. From the results presented in Table I, it is seen that the activity of ^{32}P in terminal meristems was higher following injection, even at the low dose rate of 0·375 mc. per tree, than where very high dose rates had been applied to roots. The first sample taken 24 hours after treatment showed that, following absorption through roots, dose level had very little effect on tissue activity. This probably indicates that above a certain level of activity the solution applied is injurious to the absorbing areas of the root, with resultant limited uptake, whereas at the lower dose rates preferential uptake of phosphate ions may have operated.

Table I.

Activity of ^{32}P in μc per gm. dry weight in terminal meristems following different methods of application (treated 5th May).

Root uptake			Injection			
Dose in mc per tree	Date of sample		Dose in mc per tree	Date of sample		
	6th May	13th May		6th May	13th May	26th May
12·40	0·007 (27·27)*	0·48 (20·39)	4·00	1·25 (8·38)	—	3·35 (3·20)
12·40	—	1·54 (9·02)	4·00	2·69 (8·38)	—	5·92 (3·20)
0·80	0·004 (1·01)	—	1·125	3·35 (2·32)	8·84 (1·65)	—
			0·375	0·88 (0·76)	—	0·50 (0·30)

* Figures in brackets denote activity expected with total uptake and uniform distribution throughout the plant.

Over a period of 7 days from the date of the first sample, the activity rate in meristems increased. Following root absorption, the level reached only between 2·5 and 16 per cent. of that expected from complete uptake and uniform distribution of the phosphorus, whereas the activity rate in injected trees showed a marked excess over the expected value. In two cases where uptake of solution had been

rapid, the activity rate was in excess of the calculated value after 24 hours following injection, indicating the very rapid accumulation of the phosphorus in the meristematic regions.

Variations in the activity in terminal meristems of injected trees may depend on their relationship to the point of injection, and to the transpiration stream. Table II shows that a branch emerging below the point of injection possessed a surprisingly high activity rate as compared with those arising at a higher level. When an individual branch was injected, the downward transport of the phosphate into the trunk occurred very rapidly before it entered the upward stream and became incorporated in the growing points of upper branches. Within certain limits, therefore, the actual site of injection does not materially affect the pattern of distribution of radioactivity.

Growing points of branches arising close to the point of injection and in the direct line of the upward transport of the injected solution tend to show higher concentrations of ^{32}P activity. This is exemplified in Table III where, although no general constancy of pattern emerges as between one tree and another, differences of the order of 200 per cent. between meristems of high and low branches were recorded. The variation between trees in respect of the distribution of activity is simply a

TABLE II.

Variation in ^{32}P activity (μc per gm. dry weight) in terminal meristems 24 hours after injection.

Branch		Dose in mc			
		4·0	4·0	1·125	0·366
Above point of injection	1	0·38	4·25	2·00	0·50
	2	1·27	1·29	2·06	1·68
	3	2·11	2·53	—	0·47
Injected		—	—	3·35	—
Below point of injection ..		—	1·75	—	—

TABLE III.

Distribution of ^{32}P activity (μc per gm. dry weight) in relation to position of terminal meristems.

Position		Tree A		Tree B		Tree C		Total activity
		Dose in mc 5th May	Activity 26th May	Dose in mc 5th May	Activity 26th May	Dose in mc 5th May	Activity 26th May	
Uppermost	1	4·0	3·35	4·0	5·92	0·375	0·50	9·77
Intermediate	2	,,	3·62	,,	4·02	,,	0·23	7·87
	3	,,	7·14	,,	5·60	,,	1·97	14·71
Lowest	4	,,	7·79	,,	3·29*	,,	0·82	11·90

* Below point of injection.

measure of variability in the type and density of branching. Where all branches arose at approximately the same level and at some distance away from the point of injection, the distribution of ^{32}P was fairly uniform between branches, whereas trees with irregularly placed branches and injected near the source of the lowest branch, e.g. A in Table III, showed a wide fluctuation in activity.

Concentration of ^{32}P in various tissues.

It has already been indicated in Table I that the distribution of injected phosphorus reaches a higher concentration in the meristematic regions than is expected from uniform distribution. In order to assess the chances of recovering mutants in propagated material, the relative dose in various meristematic areas was more precisely determined. Table IV illustrates that there was no substantial difference between terminal and lateral (spur) meristems, and that the variability from branch to branch was too high to enable any conclusion to be made on dose rate relative to

TABLE IV.

Distribution of ^{32}P activity (μc per gm. dry weight) in relation to injection site and position of meristems; dose of 1·125 mc injected on 5th May, sampled on 26th May.

Position*	Injected branch			1st branch above injected branch		2nd branch above injected branch	
	Wood	Terminal meristem	Lateral meristem	Terminal meristem	Lateral meristem	Terminal meristem	Lateral meristem
1	2·49	8·24	7·87	9·66	10·42	7·39	9·29
2	1·90	7·54	5·96	10·71	11·84	5·47	10·36
3	1·78	7·62	10·03	8·22	4·99	—	5·25
4	0·98	—	12·26	—	7·05	—	—
5	1·26	—	—	—	—	—	—

* 1–5, tip to base of branch.

position on the branch. In one instance the activity of the lower-placed lateral meristems was over 50 per cent. greater than that of the ones nearer the apex, while, in the branch immediately above, the trend was opposite. The activity in woody tissue varied from approximately 30 per cent. of that in the meristematic area at the apex of the injected branch to approximately 8 per cent. at the base of the branch. The decrease of activity in the wood from the apex to the base of the trees is also confirmed by the total assays recorded in Tables IX and X.

The concentration of activity in wood and bark detailed in Table V indicates that no overall difference existed between these tissues in the amount of ^{32}P accumulated. The difference in total activity from the 1·125 mc dose is a reflection of difference encountered at one position only and this is due to errors of random sampling.

The radiation in individual leaves along a rapidly elongating branch tip (Figs. 2 and 3) showed two areas of high concentration. Fig. 2 shows that the basal more mature leaves and the sub-terminal primordial leaves contained 2–3 times as much

PLATE I

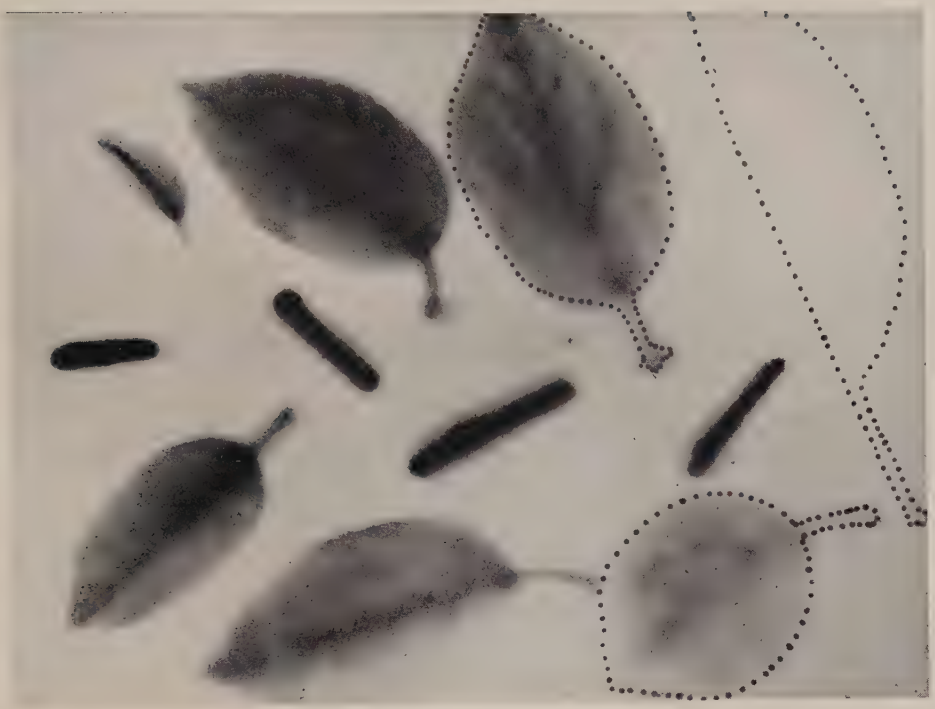

Fig. 3.

Auto-radiograph of upper part of a growing shoot with high concentration of ^{32}P in the terminal region. The outlines of the lower leaves on the radiograph had to be dotted because of their low rate of activity.

Fig. 1.

Technique of injecting solutions of radioactive phosphorus into trees.

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TABLE V.

Distribution of ^{32}P activity (μc per gm. dry weight) in wood and bark tissue; injected 5th May, sampled 26th May.

Position		1·125 mc dose		0·375 mc dose	
		Wood	Bark	Wood	Bark
Tip	1	0·425	1·099	0·1001	0·0619
Intermediate	2	—	—	0·0816	0·0944
	3	—	—	0·0709	0·0709
Injection site	4	0·150	0·175	0·0370	0·0430
Intermediate	5	—	—	0·0952	0·0764
Base	6	0·175	0·175	0·0862	0·0620
Total		0·750	1·449	0·4710	0·4086

radioactivity as those at intermediate nodes. These two regions of concentration probably coincide respectively with phases of high metabolic and high mitotic activity. If axillary buds received doses comparable to those of the subtending leaves, the frequency of mutation might be expected to vary considerably according to the stage of development of the nodes at the time of injection.

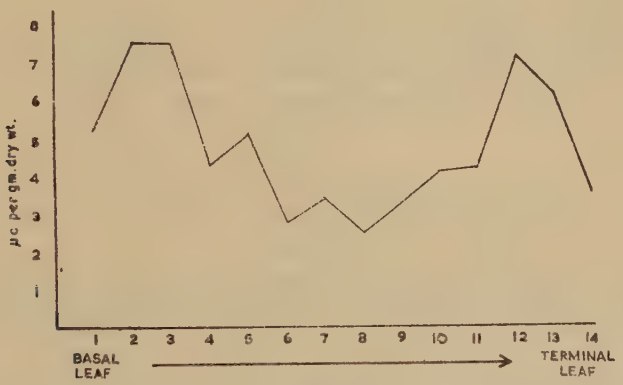

FIG 2.

Distribution of ^{32}P in leaves along a growing terminal shoot.

The accumulation of radioactive phosphorus in floral parts was of the same order as that found in vegetative meristems. At the time of injection most of the flowers were nearly open, and the samples which were taken seven days later represented fully mature flowers. At this stage maximum activity was found in the pedicel and receptacle (11·07 μc/gm.) which had twice the radioactive phosphorus content of anthers and petals. Clearly the concentration of the mutagen reaching both the ovule and pollen grain was very high and, although some radiation damage to the corolla became visible at the higher concentrations, no premature abscission of flowers was observed.

Activity in relation to numbers of active buds.

From the results presented so far it is clear that, since much of the ^{32}P supplied is concentrated in the meristem, the dose per tree must be regulated to provide a sub-lethal dose in such areas. The amount of any given dose that finally reaches the meristem will depend on the total weight of the plants and on the number of meristematic regions competing for the supply. In an attempt to assess the optimum dose level, trees of uniform size and with known bud numbers were injected with solutions containing varying concentrations of radioactive phosphorus. The results of these experiments are set out in Tables VI and VII and in Fig. 4.

TABLE VI.

Activity of ^{32}P (μc per gm. dry weight) in terminal meristems in relation to number of active buds.

No. active meristems	Dose mc per tree (injected 5th May, sampled 14th May)						
	7·0	3·5	1·67	0·84	0·42	0·21	Total
12	103·7	134·5	17·0	10·9	22·3	4·8	293·2
24	116·3	38·3	43·9	23·2	7·1	2·9	231·7
48	56·6	32·3	18·5	22·5	4·0	1·7	135·6
96	57·6	20·5	6·0	1·5	3·0	2·9	91·5
n*	32·3	45·3	0·7	7·9	2·2	2·8	91·2
Total	366·5	270·9	86·1	66·0	38·6	15·1	

* Number of buds not counted.

TABLE VII.

Activity of ^{32}P (μc per gm. dry weight) in terminal meristems in relation to the number active buds.

No. active meristems	Dose mc per tree (injected 5th May, sampled 25th July)						Total
	7·0	3·5	1·67	0·84	0·42	0·21	
12	—	—	0·115	0·045	0·054	—	—
24	—	0·189	0·091	0·048	0·052	0·031	—
48	0·135	0·104	0·108	0·051	0·028	0·019	0·445
96	0·093	—	0·060	0·021	0·032	—	—
n*	0·128	0·208	0·053	0·016	0·015	0·020	0·440
Total	—	—	0·427	0·181	0·181	—	

* Number of buds not counted.

It is seen from the totals set out in Table VI, where individual treatment fluctuations due to sampling errors have been minimized, that halving the dose resulted in an approximately proportional reduction in activity at the meristem, while an eightfold increase in bud number reduced the activity by more than 50 per cent. The regression lines in Fig. 4 indicate that when comparison is made between

trees with 12 and 96 buds, doubling the administered dose for the higher bud number results in approximately equivalent dose rates in the meristems. When treatments bearing 48 buds are compared with those having 96 buds, the regression lines are very similar, indicating that at the higher bud numbers changes in activity rate per unit of dose do not vary appreciably with changes in bud number. At the lowest dose rate of 0·21 mc per tree the activity recovered showed no variation according to bud number over the range 24–96 buds. Similarly the variation in activity in plants with 96 buds over the three lowest dose rates was entirely due to errors of sampling. These two facts show that, when the administered dose is low in relation to the number of active buds, the increase in activity rate is not proportional to the dose, and that there must be preferential absorption of phosphorus by the meristem when the concentration falls between certain limits of availability.

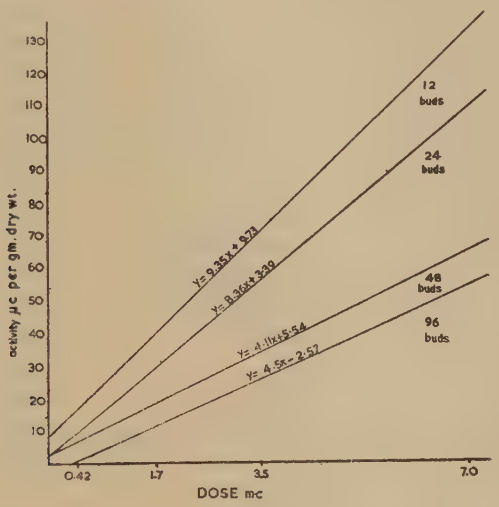

FIG 4.

Regression of activity rate on dose in relation to numbers of active buds.

Lethal damage from radiation was observed only in those experiments with the three treatment combinations : 7 mc dose, 12 buds ; 3·5 mc dose, 12 buds ; 7·0 mc dose, 24 buds. At these three levels, when the radioactivity exceeded 100 μc per gm. dry weight, the upper branches died and the tree produced new branches from dormant buds situated below the level of branching. In no other treatment was any severe form of damage observed. Treatments with recorded activity above 50 μc per gm. dry weight showed a varying degree of necrosis of young leaves, but no marked reduction in growth rate or outward damage to axillary or terminal buds was observed at these levels.

Clearly, therefore, the optimum dose for trees similar to those used in the present investigations bearing from 80–150 active buds at time of injection, and having a tolerance level of about 50 μc per gm. dry weight, varies between 3·5 and 7·0 mc per tree. Optimum doses for material bearing different numbers of active buds can be similarly derived from the data.

The figures set out in Table VII show the activity rate in terminal meristems of the same trees as those recorded in Table VI, after a period of growth extending over 72 days. The chief point of interest in Table VII, as compared with Table VI, centres around the comparative uniformity of the data irrespective of dose level or bud number. Comparison of the totals for 48 and " n " bud numbers, and for 0·84 and 0·42 mc dose levels in Tables VI and VII will serve to bring out the general trend. This can only mean that at high activity rates, comparatively more of the ^{32}P is lost from the tissues. This loss cannot be entirely accounted for by increased growth, since the necrotic effects developed at the upper levels of radioactivity indicate a greater growth injury at these levels. It seems therefore that excess of phosphorus is continually being exuded by the plants through the roots and possibly also through the leaves. Evidence of root exudation is presented later. In view of this, the radiation dose received by the meristems throughout the effective life of the radioactive substance must be considerably less than the dose calculated at the time of assay shortly after injection, and the higher the activity rate attained the larger must be the discrepancy between the physical and biological half-life of the isotope.

Table VIII gives the mean activity for all bud numbers at three different dose levels after a growth period of 72 days. The expected activity was calculated from the mean activity on 14th May corrected for a 72-day period of decay. The actual ^{32}P content on 25th July ranged from 10 to 16 per cent. of that expected when only the physical decay rate is considered. The loss of activity that was brought about by growth and exudation was, therefore, relatively very high. Unfortunately the figures in this table are not sufficiently comprehensive to enable a precise comparison to be made of relative mean loss of ^{32}P in relation to dose rate.

TABLE VIII.

Activity of ^{32}P (μc per gm. dry weight) in terminal meristems following a growth period of 72 days.

Dose in mc	Mean activity 14th May	Mean activity 25th July	Expected activity 25th July	Actual ÷ expected
1·67	17·08	0·085	0·530	0·16
0·84	11·62	0·036	0·361	0·10
0·42	7·28	0·036	0·225	0·16

Total assay of injected trees.

The distribution of radioactivity throughout the entire tree, as well as in the soil substrate in which injected trees were grown, gives a complete picture of the ultimate fate of the injected dose and provides a reliable guide to the efficiency of the dose rate in terms of the proportion of the total dose that is recovered in active buds. Table IX and Fig. 5 summarize the results obtained.

In most cases the total amount recovered agreed to a surprisingly high degree with the injected dose. The one exception is the treatment (Table IX) with low dose and high bud number. No explanation can be advanced to account for this

TABLE IX.

Total distribution of ^{32}P activity in relation to dose and number of active buds; injected 8th May, sampled 14th May, assayed 27th June.

Material	3·69 mc dose								0·22 mc dose							
	12 buds				96 buds				12 buds				96 buds			
	Total dry wt. (gm.)	μc/gm.	Total μc	% Activity	Total dry wt. (gm.)	μc/gm.	Total μc	% Activity	Total dry wt. (gm.)	μc/gm.	Total μc	% Activity	Total dry wt. (gm.)	μc/gm.	Total μc	% Activity
Leaf ..	8	36·53*	35†	10·44	50	20·00*	120†	40·95	5	3·33*	2†	9·52	37	2·25	10	32·25
Branch ..	128	3·31	51	15·22	733	0·83	73	24·91	200	0·29	7	33·33	478	0·08	5	16·13
Trunk ..	256	5·50	169	50·44	419	0·41	25	8·53	218	0·08	2	9·52	318	0·16	6	19·35
Root ..	416	1·25	62	18·50	966	0·41	48	16·38	404	0·12	6	28·57	556	0·08	5	16·13
Soil ..	6,810	0·02	18	5·37	1,360	0·16	27	9·21	6,810	0·005	4	19·04	13,620	0·003	5	16·13
Total ..	—	—	335	—	—	—	293	—	—	—	21	—	—	—	31	—
Amount recovered	335 × 10·6157‡ = 3·56 mc				293 × 10·6157 = 3·11 mc				21 × 10·6157 = 0·22 mc				31 × 10·6157 = 0·33 mc			

* Corrected for 44 days' decay. † Activity on 27th June. ‡ 49 days' decay factor.

discrepancy. The proportion of the total dose recovered in leaves of plants with very few bud numbers was very small even at the lowest dose rate of 0·22 mc per tree. An increase in bud number from 12–96 resulted in an increase of between 300–400 per cent. in the recovered activity, while over the same range the concentration of ^{32}P per gram was reduced by slightly less than 50 per cent. Similarly at low bud numbers a much higher proportion was found in the woody regions such as branches, trunk and root. It is noteworthy that as early as 6 days after injection, up to 28 per cent. of the total activity resided in the root and large amounts varying from 5–19 per cent. had been exuded into the soil in this comparatively short period of time.

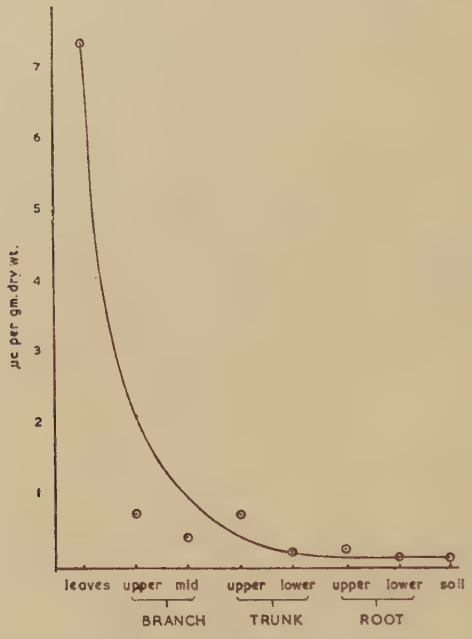

Fig 5.

Distribution of ^{32}P throughout whole trees and in the soil.

The same general trend is seen in Table X and Fig. 6 which record the total assay of trees 79 and 72 days respectively after injection. Two dose rates are here compared in trees with similar bud numbers. The relative activity of the meristems was still high but the proportion of the total that was recovered in soil rose as high as 36 per cent. Also the activity rate per gram of soil showed far less reduction during the period than the activity rate in the tissue, which can only mean that the amount in the soil had been continually replenished by exudation from the root surfaces. It seems, therefore, that a large part of the excess phosphorus found its way out of the plant and that little replenishment from the wood to the growing tip occurred to increase and maintain the activity rate during growth.

TABLE X.

Total distribution of ^{32}P activity 79 days after injection, in relation to dose; injected 8th May, sampled 26th July.

Material	Dose, 3·69 mc ; 24 active buds				Dose, 1·67 mc ; 24 active buds			
	Total dry wt. gm.	μc/gm.	Total μc	% Activity	Total dry wt. gm.	μc/gm.	Total μc	% Activity
Leaf	70	0·178	12·46	17·80	93	0·138	12·86	35·57
Branch	316	0·031	9·68	13·83	305	0·011	3·36	9·29
Trunk	545	0·025	13·63	19·47	230	0·009	2·07	5·72
Root	1,500	0·008	12·00	17·14	520	0·009	4·68	12·94
Soil	11,113	0·002	22·23	31·75	6,590	0·002	13·18	36·42
Total	—	—	70·00	—	—	—	36·15	—
Amount recovered ..	70×45·1875*=3·16 mc				36·15×45·1875=1·63 mc			

* Corrected for 79 days' decay.

INJECTION OF ^{32}P INTO HERBACEOUS SPECIES.

The results presented in Tables XI and XII are from experiments involving flowering plants of foxglove. Results obtained with sweet peas were very similar to those recorded for foxglove and need not therefore be presented. Dose rates above 1 mc per plant were generally highly injurious to the tissue, but the actual level

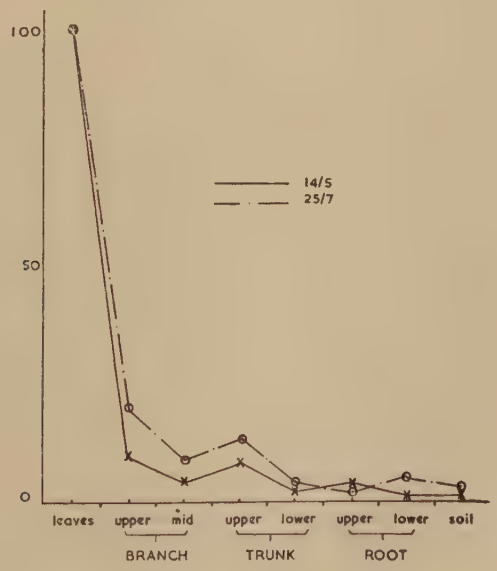

FIG 6.

Comparative distribution of ^{32}P activity following a growth interval of 72 days.

TABLE XI.

Distribution of ^{32}P (μc per gm. dry weight) 24 hours after injection into plants of foxglove at two different dose levels.

Region	0·9 mc dose				1·8 mc dose			
	Weight (gm.)	μc/gm.	Total activity (μc)	% Total	Weight (gm.)	μc/gm.	Total activity (μc)	% Total
Spike apex	3·2	11·03	21·96	75·56	6·0	13·33	52·29	81·29
Spike upper part		3·85				7·53		
Spike lower part	3·0	1·67	5·43	18·68	6·0	2·18	6·73	10·46
Root		0·87				0·07		
Soil	454	0·003	1·67	5·74	679	0·008	5·30	8·24

TABLE XII.

Distribution of ^{32}P (μc per gm. dry weight) in flowers of foxglove according to stage of development; dose, 0·5 mc. per plant; plants injected 25th June, sampled 26th June.

Developmental stage	Plant No.				Total
	1	2	3	4	
Open flower	35·1	31·0	33·5	28·6	128·2
Pollen grain mitosis	12·6	49·6	25·4	56·2	143·8
Meiosis	6·9	21·1	26·6	44·3	98·9
Pre-meiosis	6·9	28·4	19·2	29·2	83·7

tolerated varied considerably according to the size of the plant. It is seen from Table XI that, at both dose levels, over 75 per cent. of the administered dose was concentrated in the upper flower-bearing part of the spike. The total increase in activity per gram was not proportional to increase in dose rate, and the difference in total μc activity at the higher dose level was largely due to the difference in dry weight between the equivalent regions. The total amount exuded into the soil during the period between treatment and sampling is noteworthy—over 300 per cent. more activity was found in the soil at the higher dose rate. Part of this difference is almost certainly attributable to difference in root size, where a greater surface area of root effects a greater exudation of phosphorus. The total amount exuded at the higher dose rate and shown in Table XI was, however, too high to be accounted for entirely on this basis. This result supports the finding with fruit trees described earlier, where differential exudation was noted according to the concentration of radioactivity in the tissue.

An analysis of individual flowers set out in Table XII indicated that, particularly in the mature flower-stages, the relative activity is very high. The total radiation received by the sex cells in such herbaceous material indicates that the technique can be expected to be highly efficient and in plants with a short reproductive cycle the recovery of mutant forms in the progeny of treated parents presents no difficulty.

DISCUSSION.

The use of radioactive phosphorus provides an attractive technique for submitting large numbers of plants to Beta radiation for the production of new variation. The present experiments have shown that the introduced phosphorus accumulates in rapidly growing tissues. In the case of apple and pear trees, very high doses of up to 50 μc per gram dry weight were recorded and these did not prove lethal. It must be emphasized that the activity recorded in these experiments represents the total activity of a digest of the samples, and therefore is much in excess of the actual activity absorbed by the tissue.

The Beta particles emitted by ^{32}P have a relatively high maximum energy (1·7 MeV) and therefore are able to travel through a considerable thickness of tissue without absorption. In the absence of complete absorption, energy transfer will be below maximum and the mutagenic effect will be reduced. In the case of terminal and axillary buds, where the active meristematic area is very small, the proportion of unabsorbed radiation must be considerable. Several estimates have been made of the absorption of Beta particles from ^{32}P by different tissues and figures ranging from 50–70 per cent. have been derived for seeds and buds of trees (Spinks *et al.*, 1948 ; Ehrenberg and Granhall, 1952). Assuming that the lower of these is the better estimate, it is possible to calculate the radiation dosage determined in these investigations in terms of the roentgen equivalent physical (r.e.p.) and therefore to compare the dosage achieved with results from X irradiation. On the assumption of 50 per cent. particle absorption, 50 μc per gm. activity uniformly distributed in the tissue would yield a dose rate of 22,250 r.e.p. during the average radioactive life of 20·592 days of radio-phosphorus.* This represents a very high radiation dose and contrasts with the survival level of 6000–8000 r.e.p. calculated for ^{32}P-treated fruit trees by Ehrenberg and Granhall (1952). The discrepancy between the two estimates may be in part due to differences in methods of assaying the activity rate. The qualitative method used by Ehrenberg and Granhall is liable to greater error than the methods involving digested samples employed in the present experiments.

On the other hand the radiation dose arrived at here is probably too high, since it is calculated on a sample taken twenty days after injection and no account has been taken of the dilution in activity due to growth and exudation. Both these factors will considerably reduce the actual dose over the active life of the isotope. It was shown in Table VIII that only 10–16 per cent. of the expected activity was recorded 72 days after injection. Further comparisons of the soil activity in Tables IX and X following injection of 3·69 mc indicate that a large proportion of the initial dose had been exuded into the soil. Loss of activity due to growth and exudation will clearly take place slowly but continuously and the rate will determine the effective dose. We may conclude, therefore, that the dosages calculated in these experiments for fruit trees are substantially higher than the effective dose rates, possibly by as much as a factor of 2. Owing to there being so many unknown factors the approximate nature of the estimates must be emphasized.

In experiments with X-irradiation the tolerance levels that have been reported vary from 5000 r for dormant scions, where lethality appeared to be determined not so much by death of the tissue as by failure of graft union, to 25,000 r for dormant

* 1 μc of ^{32}P with average particle energy of 0·70 MeV yields 890 r.e.p. in 20·592 days when uniformly distributed and completely absorbed in 1 gram of tissue.

seeds (Ehrenberg and Granhall, 1952 ; Gustafsson and MacKey, 1948). It appears, therefore, that the energy transfer that is possible with ^{32}P treatment is well within the order of magnitude that is possible with successful X-ray dosage.

In this latter connection the relatively small amount of damage to shoots encountered in the present experiments is of considerable interest. Except at the high dose rate of 7·0 mc per tree and with low bud numbers, no loss of terminal or lateral growths due to killing of the tissue was noted. In addition the numbers of morphological abnormalities were too slight to merit attention. In consequence a series of 2,000 viable buds have been propagated for the recovery of mutations, from tissue subjected to high radiation intensity.

SUMMARY.

1. Trees of apple and pear and plants of foxglove, sweet pea, and tomato have been treated with solutions containing varying quantities of radioactive phosphorus in the form of irradiated sodium dihydrogen phosphate.

2. The rate of uptake through the root proved to be too slow and the activity attained in the tissue too low to merit its consideration as an effective method of treatment for achieving high radiation dosage.

3. Methods of injection into woody and herbaceous tissues are described which permit an accumulation of phosphorus in the meristematic areas up to a level which is in excess of the lethal dose.

4. Rapid transport in all directions from the injection site was demonstrated and, within limits, the position of entry of the radioactivity did not materially affect the final distribution. The rate and extent of downward transport of the phosphorus was shown to be an important factor in influencing the effective dose at the growing points.

5. Meristematic regions showed rapid accumulation of phosphorus far in excess of the quantity expected from uniform distribution. The activity attained in such areas at low dose levels was not proportional to the administered quantity, while at the higher activity levels the biologic half-life of the isotope was considerably reduced when compared with the lower concentrations.

6. The efficiency of the dose was shown to be directly related to the number of active buds. At the higher bud numbers, a higher proportion of the injected dose was recovered in the growing points and, when activity levels in trees with 12 and 96 buds were compared, approximately equal activity rates were attained by doubling the dose applied.

7. Loss of activity in the meristems was shown to be brought about by exudation through the root as well as by dilution due to growth. The possibility of exudation through the leaf surface was not tested.

8. The upper levels of tolerance of vegetative buds of apple and floral buds of foxglove, calculated as total activity shortly after injection, were approximately 50 and 12 μc per gm. dry weight respectively. These correspond to doses of 44,500 and 10,600 r.e.p., if total absorption of particles is assumed. If absorption is taken to be 50 per cent. and if the biologic half-life at these high levels is about a half of the physical half-life, the calculated total doses at the upper tolerance limits are reduced to 11,000 and 2,500 r.e.p. for the two types of material.

9. By reason of the rapid accumulation of ^{32}P in the vegetative and floral meristems, and of the comparatively low irradiation damage suffered by the material at high dose rates, the use of ^{32}P could prove extremely valuable for increasing the mutation rate, particularly in plants which do not lend themselves to large-scale irradiation from other sources, such as X-rays and neutrons.

ACKNOWLEDGMENTS.

We wish to express our gratitude to Dr. N. G. Trott, Institute of Cancer Research, for invaluable guidance on equipment and counting techniques, and to Dr. K. S. Dodds, Director, John Innes Horticultural Institution, for his continued interest and encouragement.

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(*Received* 6/5/57.)

THE INCIDENCE AND CONTROL OF CANE SPOT (*ELSINOË VENETA* (BURKH.) JENK.) ON LOGANBERRY

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THE name " Cane Spot " is more appropriate to this disease on raspberry than on loganberry, on which the most obvious symptom is infection of the leaves, though the young canes and even the berries can sometimes be severely infected. It is, however, convenient to retain the same name for the disease on either host ; in the U.S.A. the corresponding disease on both hosts is usually referred to as Anthracnose.

The lesions, already described for raspberry in England (Harris, 1931), are similar on loganberry, on which the chief damage arises from leaf impairment and defoliation following a severe attack. The fungus overwinters on cane lesions, as in raspberry, and the apical parts of canes may sometimes be killed by cankering.

CONTRASTS BETWEEN RASPBERRY AND LOGANBERRY AS AFFECTING SPRAY TREATMENT.

In raspberry, ascocarps develop in quantity on surface lesions on the fruiting canes from February onwards, and in most seasons mature ascospores can be found from the end of March (Harris, 1931). They are airborne, are forcibly discharged, and are responsible for most, if not all, of the early infections that develop usually towards the end of May on the young canes growing up amongst the vertical fruiting canes and thus forming a convenient target. Later, conidia, which are mucilaginous and water-borne, yield secondary infections on leaves and canes.

The essence of good control lies in combining the destructive effect on the ascocarps of a fungicide applied to the fruiting canes when the buds are bursting, with the protective effect on the young canes and foliage of a fungicide applied just before blossom. Results vary with the season, but usually the first spray is the more important (Harris, 1931 ; Cadman, 1950).

In loganberry, ascospores appear to play a less prominent part in the annual infection cycle. Ascocarps containing mature asci and spores can be found in summer on surface lesions on the fruiting canes, but they have not consistently been seen in the quantities usually associated with raspberry, and sometimes not at all.

The natural procumbent habit of the fruiting canes of loganberry ensures that for the most part they are held well away from the young canes developing at the basal centre of the plant, where the fruiting canes are usually not carrying over-wintered inoculum. Infection is thus likely to be, and is, at first confined to the leaves on the developing fruiting laterals near the distal cane lesions, and not to the young canes, as in raspberry. Later, when the young canes are long enough, their foliage is nearer to or may mingle with these sources of infection, and ascospore or conidial infection readily ensues in favourable weather.

The bearing that this has on the influence of methods of arranging the growing new canes on the wirework is obvious. As regards spray treatment, the emphasis would appear to be on protecting the young leaves and canes rather than on impairing the ascocarps directly by a spray applied to the fruiting canes early in the season, as in raspberry. Wade (1949), however, recommends green-tip and pre-blossom sprays for both host plants in Tasmania, but in England the bud-burst spray recommended for raspberry had proved ineffective on loganberry (Harris, 1932). The results of exploratory experiments to devise a satisfactory spray programme for this host (Harris, 1933 ; Harris and Hamond, 1934 ; Harris, Moore and Steer, 1935 ; Steer, 1935 ; Harris, Beakbane and Moore, 1940) were utilized by Beakbane (1941) in a cultural comparison of two closely related crop plants, loganberry and Phenomenal berry, but it was not possible to include a comprehensive study of the spraying issue. The experiments to be described were therefore designed to find the minimum effective spray programme in terms of two widely contrasted methods of training the young canes on the wirework.

Experimental methods.

Training the young canes.

Clonal loganberries, raised as rooted tips, were planted *in situ* in spring, 1938, at 10 ft. apart in seven North to South rows 6 ft. apart. The even-numbered rows were buffers for spray-drift from the four treated ones, and there were buffer plants between plots and at the ends of the rows. In the four experimental rows, the young developing canes were trained by either of two methods :

Method I, first vertically, then horizontally above the fruiting canes, and therefore above this source of inoculum (Beakbane, 1941). The buffer plants were all trained in this way.

Method II, horizontally below the fruiting canes, and thus in the most favourable position to receive spore-inoculum washed downwards by rain. This is, however, the more labour-saving method.

During their growing season the young canes were loosely tied together in two bunches, one on each side of the plant, and supported either by the top (6 ft.) or bottom one (2 ft.) of five equidistant horizontal wires, according as the first or the second method was being followed. Early the next year (usually in February), in which these canes were due to crop, they were woven and secured to the three middle wires (Beakbane, 1941, Method (iv)). These fruiting canes were cut out after cropping and thus made way for the current-year canes to be woven in their place.

Spray treatments.

These were arranged in a 4 × 4 Latin square and applied to six-plant plots, three plants trained by Method I and three by Method II. Fungicidal sprays were applied from 1938–43 as follows :

A, nil (*controls*) ;
B, about the end of August soon after all the crop had been picked (*post-crop*) ;
C, just before the blossoms opened (*pre-blossom*) ;
D, first about mid-May (C, *pre-blossom*) and again towards the end of June as the first berries were ripening (*pre-ripening*), when an insecticide (derris)

for Raspberry Beetle control is recommended (Steer, 1934). This is commonly known as " the beetle spray ".

Freshly-made Bordeaux mixture at 4 lb. copper sulphate and 6 lb. hydrated lime in 100 gallons water (4–6–100) was used pre-blossom, and a manufactured copper-oxychloride spray (15 per cent. Cu) at 0·33 per cent. by weight (=0·05 per cent. Cu), with derris (approximately 2·7 per cent. rotenone) at 0·2 per cent. by weight (=0·005 per cent. rotenone) and a wetter (soap, made in the tank from caustic soda and oleic acid) for beetle control. Bordeaux mixture was not used in the beetle spray, to preclude an unsightly deposit on the berries.

As the copper oxychloride spray consistently depressed the crop, the treatments were modified for the period 1944–6 to see whether or not a half-strength suspension, coupled with re-arrangement of the spray programmes, would eliminate spray damage without impairing Cane Spot control. The following fungicide treatments were therefore randomized on the earlier experiment in such a way that any cumulative effects of the previous treatments could be detected and allowed for :

(1) nil (*controls*) ;
(2) copper oxychloride at 0·025 per cent. Cu, i.e. half the strength used in the previous trial, and applied twice, first immediately after flowering (*post-blossom*), and then, as before, at the end of June, when the first berries were ripening (*pre-ripening*) ;
(3) freshly-made Bordeaux mixture at 4–6–100 (*pre-blossom*), followed by half-strength copper oxychloride when most blossoms were over, usually in the first half of June (*post-blossom*) ;
(4) as (3), but with the second spray at " the beetle stage " at the end of June (*pre-ripening*). This treatment was the same as D in the earlier trial except that the oxychloride spray was at half-strength.

Derris with soap was applied twice, post-blossom and pre-ripening, to ensure maximum effect against the beetle. The critical treatment was No. 2 ; Nos. 1 and 4 kept continuity with the original experiment, and No. 3, though including the single-purpose pre-blossom spray, was designed to show the effect of shortening the interval between sprayings when compared with No. 4.

The differential cane-training methods were continued during this period but, as the main emphasis was on the modified spray treatments, less frequent attention than hitherto was given to Training Method I.

The sprays, at 250–300 p.s.i. pressure, were applied mostly from a mobile 2 h.p. machine through a lance with two or three nozzles. The beetle spray of derris and soap was applied to all plants irrespective of fungicide treatment.

Records.

Cane Spot. Foliage infection was recorded, mostly on the fruiting canes, two or three times every season and beginning in July. The plants were classified separately on their East and West sides into one or other of the following categories :

0, no or very slight infection ;
1, up to light general spotting, or two or three small but concentrated patches ;
2, light to moderate general spotting with a few concentrated patches ;
3, moderate general spotting with several concentrated patches ; infected foliage obvious ;

4, moderate to severe general spotting with many concentrated patches ;
5, very severe infection of 75 per cent. or more of the leaves on the fruiting laterals ; few, if any, non-infected.

Leaf-bronzing. This conspicuous effect of copper sprays was observed every year and records were made in 1943. A category figure was allotted to each plant over the broad range :

0, none ;
1, slight ;
2, slight to moderate ;
3, general over most of the plant.

RESULTS.

In the following tables, the figures represent mean category values per plant except where otherwise stated. For convenience of presentation and discussion, the data are appropriately combined to show in turn the influence of spraying, training, and aspect, and also of any interaction between them. The final record on the fruiting canes each year shows the maximum level attained by the disease before these canes were cut out in the normal course of husbandry. Records on the young canes in autumn show the level of disease carried over from one season to the next.

Significance levels of difference from unsprayed controls are shown by the following convention :

†, $P<0.1$ **, $P<0.01$
*, $P<0.05$ ***, $P<0.001$

Table I.

Cane Spot infection (1939–43) on leaves of young canes (Y) and fruiting canes (F) in relation to spray treatments.

Recorded		Canes	Spray treatment (1938–43)			
			A. Unsprayed	B. Post-crop	C. Pre-blossom	D. Pre-blossom and pre-ripening
1939	27th Oct.	YF	0·50	0·13**	0·41	0·22*
1940	11th Oct.	F	1·52	0·92†	0·68*	0·65*
1941	29th Aug.	F	2·19	1·98	1·41***	0·90***
		Y	1·10	1·10	0·63†	0·17**
1942	1st Sept.	F	2·43	2·55	1·75**	1·08***
		Y	1·43	1·40	0·80**	0·23***
1943	15th July	F	2·52	2·58	0·80***	0·30***
	10th Aug.	F	3·00	3·03	1·13***	0·70***

Response of the disease to spray treatments.

Clearly the best control came from two sprays (Table I, D), the first applied just pre-blossom and the second as the earliest fruits were colouring, but a single

pre-blossom spray (C) also gave a high degree of control in most cases. The post-crop spray (B) showed promise at the outset, but not afterwards. By 1941 the disease was well established in this plot and in October of that year abundant infection was recorded on the leaves of the overwintering young canes (mean category value per plant, 2·34 ; all plants). If used following earlier sprays, the post-crop spray could check mounting infection, especially in a wet autumn, when the earlier spray-deposits have weathered.

TABLE II.

Cane Spot infection (1944–6) on leaves of fruiting canes in relation to spray treatments.

Recorded		Spray treatment (1944–6)			
		1. Unsprayed	2. Post-blossom and pre-ripening	3. Pre-blossom and post-blossom	4. Pre-blossom and pre-ripening
1944	12th Sept.	2·2	1·1*	0·9*	0·9*
1945	7th Aug.	2·3	1·2***	1·0***	1·0***
1946	26th Aug.	3·0	2·3†	1·0**	1·2**

The pre-blossom Bordeaux spray, included in treatments 3 and 4 (Table II), can evidently be a stabilizing influence in the control of this disease in some seasons. In 1944–5 its omission was not detrimental when two post-blossom sprays were given (No. 2), but these did not compensate similarly in the wet summer of 1946. When the pre-blossom Bordeaux was given, however, it made no difference whether the post-blossom spray was applied just after flowering (No. 3) or just before the fruits ripened (No. 4).

Response of the disease to cane-training methods.

Training the young canes above the fruiting canes (Method I) showed remarkable consistency in checking Cane Spot infection on the leaves of the young canes (Table III). That the effect was still evident when they were fruiting a year later

TABLE III.

Cane Spot infection (1941–3) on leaves of young canes (Y) and fruiting canes (F) in relation to cane-training methods.

Recorded		Canes	Training method	
			Young canes above (I)	Young canes below (II)
1941	29th August ..	F	1·45	1·84
		Y	0·40	1·10
	22nd October	Y	1·84	2·85**
1942	1st September ..	F	1·60	2·30
		Y	0·30	1·63
	16th October	Y	0·47	2·37
1943	15th July	F	1·23	1·86
	10th August	F	1·67	2·30

Differences are significant at $P<0.001$ except ** at $P<0.01$.

is a notable instance of the bearing of any one year's treatment on infection the following year. In this case it is not really surprising, for with Method II conidia splashed downwards in rain have a target conveniently arranged, and infection thus begun as overwintering cane-lesions continues the following year when the new leaves appear.

Response of the disease to a combination of spray treatments with cane-training methods.

The results in Table IV show that the disadvantage imposed by the less costly Method II can be offset by suitable spray treatment.

TABLE IV.

Cane Spot infection (1941–3) on leaves of young canes (Y) and fruiting canes (F); interaction effects of treatments.

Recorded		Canes	Method of training young canes	Spray treatment (1938–43) A. Unsprayed	B. Post-crop	C. Pre-blossom	D. Pre-blossom and pre-ripening
1941	29th Aug.	F	II (below)	2·46	2·58	1·50	0·83
			I (above)	1·92	1·37	1·55	0·96
			II–I	*0·54*	*1·21***	*−0·05***	*−0·13***
		Y	II	1·60	1·77	0·93	0·10
			I	0·60	0·43	0·33	0·27
			II–I	*1·00*	*1·34*	*0·60*	*−0·17***
1942	1st Sept.	F	II	2·58	3·25	2·13	1·25
			I	2·30	1·83	1·38	0·92
			II–I	*0·28*	*1·42****	*0·75†*	*0·33*
		Y	II	2·33	2·57	1·33	0·33
			I	0·57	0·23	0·23	0·17
			II–I	*1·76*	*2·34*	*1·10†*	*0·16****
1943	15th July	F	II	2·92	3·13	1·08	0·33
			I	2·13	2·05	0·50	0·25
			II–I	*0·79*	*1·08*	*0·58*	*0·08**

Plants sprayed twice (D) showed the least influence of the method of training on infection, i.e., adequate spray treatment compensated for the potential increase in infection arising from training by Method II. It should be noted that the post-crop spray (B) showed to slight advantage over no spraying when helped by Method I—a fact obscured by another arrangement of the data (Table I), in which only the overall effect of spraying was examined. With Method II, infection was evidently already too well established for the post-crop spray to control it ; indeed, infection was even greater here than on the unsprayed plants.

By contrast, the single pre-blossom spray (C) showed merit even when coupled with Method II—a tribute to an early start when circumstances are weighted against the spray. Nevertheless, the need to support it later is evident, for when a pre-ripening spray was added (D), both early and, to some extent, late infection were controlled, and might have been eliminated by the further addition of a post-crop spray (B) to deal with late-season increment.

Influence of aspect on the incidence of the disease.

It was obvious at an early stage in the trial that infection was greater on one side of the plants than on the other, so the two sides (E. and W.) were separately recorded (Table V).

TABLE V.

Cane Spot infection (1940–3) on leaves of young canes (Y) and fruiting canes (F) in relation to aspect.

Recorded		Canes	Aspect		Sig. at
			E.	W.	
1940	11th October	F	1·16	0·80	P<0·001
		Y	0·80	0·53	P<0·01
1941	29th August ..	F	1·75	1·54	P<0·05
1943	10th August ..	F	2·27	1·70	P<0·001

Significantly more Cane Spot was present on the east side of plants than on the west, which accords with a similar observation made for Apple Scab (Moore, 1936) and probably reflects slower drying of surface moisture on the east side. This response to meteorological environment was occasionally modified by the method of training, as shown for example by the data from the fruiting canes for 11th October 1940, when shade provided by the foliage of young canes overtopping the fruiting canes was probably responsible for an increase in infection on the west side (I, W.), yielding a significant (P<0·05) interaction response between aspect and training method :

Aspect	*Young canes above (I)*	*Young canes below (II)*
E.	1·17	1·15
W.	0·95	0·65
E.–W.	*0·22*	*0·50*

Influence of sprays and training methods on the host plant.

Incidence of leaf-bronzing. The copper oxychloride applied post-blossom in June and, to a less degree, the Bordeaux mixture applied pre-blossom caused conspicuous bronzing of the leaves, especially those on the fruiting canes (Table VI). Weakly plants showed more bronzing than vigorous ones.

Leaf-bronzing in 1943, present to some extent in the absence of spray treatment (A and B), increased with increase in the number of pre-crop sprays, and it was not reduced in 1944 when the strength of the copper oxychloride spray was halved ; indeed, it was more extensive even on unsprayed control plants in 1944 than in 1943, so weather conditions were evidently responsible for some of it.

Where the young canes had been arranged above the fruiting canes in 1942, the degree of foliage bronzing on these canes when fruiting *in 1943* was significantly greater (P<0·01) than where the young canes had been below the fruiting canes

Table VI.

Effect of sprays on the incidence of leaf-bronzing on fruiting canes.

Spray treatment (1938–43)	Bronzing 15th July 1943	Spray treatment (1944–6)	Bronzing 14th July 1944
A. Unsprayed	0·30	1. Unsprayed	1·1
B. Post-crop	0·60*	2. Post-blossom and pre-ripening	2·2**
C. Pre-blossom	1·13***	3. Pre-blossom and post-blossom	2·4**
D. Pre-blossom and pre-ripening	2·17***	4. Pre-blossom and pre-ripening	2·7**

(above (I), 1·27 ; below (II), 0·80). To train the young canes vertically at first rather than horizontally evidently prejudiced their ability to withstand spray treatment the following year. This interpretation is supported by data on crop and cane weights, especially when interaction effects are considered.

Effect on crop. Training treatments, both irrespective of spray treatments and also when interacting with them, had a very pronounced effect on the crop (Tables VII and VIII).

Table VII.

Effect of training methods, and of their interaction with spray treatments, on the 1943 crop (lb. per plant).

Training method (1942)	Spray treatment (1938–43)			
	A. Unsprayed	B. Post-crop	C. Pre-blossom	D. Pre-blossom and pre-ripening
Young canes above (I) ..	6·33	7·10	6·17	4·67
,, ,, below (II) ..	3·33	3·50	4·57	5·43
I–II	*3·00*	*3·60*	*1·60*	*−0·76***

Table VIII.

Effect of training methods, and of their interaction with spray treatments, on total crop 1944–6 (lb. per plant).

Training method (1944–6)	Spray treatment (1944–6)			
	1. Unsprayed	2. Post-blossom and pre-ripening	3. Pre-blossom and post-blossom	4. Pre-blossom and pre-ripening
Young canes above (I) ..	17·72	16·41	14·64	16·28
,, ,, below (II) ..	10·84	12·98	11·92	11·73
I–II	*6·88*	*3·43*	*2·72*	*4·55*

Training Method I, which displays the young canes to better light and aeration than Method II, resulted in much greater crops. Some of the individual differences in 1943 can doubtless be attributed to a difference in Cane Spot infection, which had accumulated on the canes trained under Method II in the previous year (Table III). Thus the differences receded as the crop on these canes increased, through improved control of the disease by spray treatment (Table IV). But at the same time the crop from the DI plants was depressed, evidently as a result of the spray damage referred to above (Table VI), so the difference in this case was actually reversed significantly. The pre-ripening copper spray thus more than offset through spray damage an advantage in cropping potential transmitted solely by Training Method I from the previous year, but this disadvantage was obviated in 1944–6 when the strength of the copper oxychloride spray was halved.

Effect on cane weight. The fruiting canes from each plant were weighed when cut out after cropping. Spray treatments interacted with training methods to show a significant response in the vigour of the 1943 fruiting canes (Table IX), evidently due largely to cumulative effect carried over from 1942.

TABLE IX.

Interaction effect of spray treatment and training method on cane vigour expressed as fruiting-cane weight (lb. per plant), 1943.

Training method (1942)	Spray treatment (1938–43)			
	A. Un-sprayed	B. Post-crop	C. Pre-blossom	D. Pre-blossom and pre-ripening
Young canes above (I) ..	3·87	2·97	3·10	2·57
,, ,, below (II) ..	2·73	2·50	3·93	4·57
I–II	*1·14*	*0·47*	*—0·83****	*—2·00****

With Method II, but not with Method I because of spray damage, cane weight increased through Cane Spot control by the pre-crop sprays (C and D). Clearly, cropping potential (Tables VII and VIII) was largely a reflection of cane vigour, for the pattern of differential response to the interacting treatments was similar in each case.

DISCUSSION.

Over the period 1938–43 Cane Spot was well controlled by protective copper sprays applied twice, first just before blossom (*pre-blossom*) and again just before the earliest fruits ripened (*pre-ripening*); the pre-blossom spray by itself gave fairly good control. A spray applied soon after all the crop had been picked (*post-crop*) showed promise before Cane Spot became well established in the plot as a whole; thereafter it did not contribute except to a small degree where the young canes were arranged above the fruiting canes (Method I). Doubtless, however, this spray would supplement the protective effect of the earlier sprays, after these had weathered, against the

advance of late infection on the young canes in favourable conditions for it. The extra spraying entailed might nevertheless prove uneconomic, for the residuum of infection is usually small (Table I, Y, D).

In seasons 1944–6 omission of the pre-blossom Bordeaux spray hazarded the efficacy of the spray programme in a wet summer like that of 1946, though in the two other seasons its omission was compensated for by the application of two " half-strength " copper oxychloride sprays post-blossom before the crop ripened (Table II). Where Bordeaux mixture or some other copper preparation is applied pre-blossom, a single copper oxychloride spray may be given at any convenient time post-blossom before the crop ripens.

Manipulating, or training, the young canes to grow above the fruiting canes (Method I) proved of itself to be an effective way of reducing infection to a fairly low level (Table IV, Y, I A), and it must be emphasized that its influence was clearly seen a year after the treatment was applied (Table III, F, I and II). Not only was Cane Spot infection much reduced in the current year, but the vigour of the canes and the weight of the crop were increased the following year, though the one may not be solely a reflection of the other. Copper oxychloride at 0·05 per cent. Cu at the pre-ripening stage, however, vitiated these desirable responses by depressing the vigour and subsequent yield of young canes thus trained. This subtle form of spray damage had a more obvious phase in leaf bronzing. " Half-strength " copper oxychloride is to be preferred for, although leaf-bronzing is not thereby avoided*, the risk of decrease in cane-weight and crop is negligible where it would otherwise be greatest, i.e. where training Method I is adopted.

The heaviest crops invariably accrued where the young canes were arranged above the fruiting canes, except where spray damage supervened (Tables VII and VIII). Its virtual elimination as a factor in crop depression, achieved by halving the strength of the copper oxychloride, removed even that exception to the general rule. But to obtain the full advantages of Method I entails time and care, though less frequent attention coupled with a modicum of spray treatment may offer a satisfactory compromise. Good beetle control is necessary for a high-quality crop (Steer, 1934), and at least one post-blossom derris application is necessary whatever training method is adopted, so that no extra spraying labour would be entailed by including copper oxychloride in one or more combined sprays.

RECOMMENDATIONS.

Where training Method II is preferred, a spray programme is essential to ensure good Cane Spot control. The programme most likely to offer consistently good and safe control is one including freshly-made Bordeaux mixture at 4–6–100 applied pre-blossom, followed by a " colloidal " copper preparation diluted to contain 0·025 per cent. copper (or perhaps even 0·05 per cent. for plants trained under Method II) applied once post-blossom, between petal-fall and the ripening of the crop. The second of these could conveniently be timed to include a derris preparation diluted

* Some evidence was obtained from an ancillary trial not described in this paper that the inclusion of 0·75 per cent. by volume of washed cotton-seed oil with either Bordeaux mixture or copper oxychloride much reduced the tendency to foliage injury on loganberry from the copper sprays. A similar result has been recorded for cherry, plum, and apple (Montgomery and Moore, 1945).

to contain 0·005 per cent. rotenone for beetle control. As a less satisfactory alternative fungicidally, the pre-blossom spray could be omitted in favour of two post-blossom sprays of copper oxychloride, each containing 0·025 per cent. copper, and with at least the second of these derris would be included. The addition of cotton-seed oil at 0·75 per cent. by volume would reduce any risk of damage from the copper sprays, but would, of course, add to their cost.

The conclusion from the data is, however, inevitable that even with the most effective spray programme, the crop yield under Method II is unlikely to equal that from even *unsprayed* plants treated under Method I (Tables VII and VIII). The desirability of the choices offered is a matter that can be decided only by each grower in the light of his own circumstances.

SUMMARY.

The incidence of Cane Spot disease on loganberry is contrasted with that of the similar disease on raspberry.

A sequence of copper-containing sprays applied both before and after blossom gave satisfactory protection against the disease, and the method of cane-training adopted had a marked effect on the efficacy of spray treatment. More sprays were needed when the young canes were tied in below already infected fruiting canes (Method II) than when they were arranged above them during the growing period (Method I). Method I, however, rendered the canes more susceptible to spray damage in the following year, but reduction in strength of the post-blossom spray eliminated its most damaging feature, viz. an adverse effect on cropping. The most outstanding result of the experiments was the increase in crop that resulted from the adoption of Training Method I as contrasted with the less laborious Method II.

ACKNOWLEDGMENTS.

The writer is greatly indebted to Dr. R. V. Harris and Dr. A. B. Beakbane, both of whom gave freely of their advice and help during the planning and throughout the progress of these experiments ; the latter also supervised the cane-training. He is indebted also to members of the Pomology recording staff, and in the later years to Miss M. Bennett, for many of the field records, and to the Statistics Section, in particular to Dr. S. C. Pearce, for the analyses.

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(*Received* 14/5/57.)

EFFECTS OF SOIL MOISTURE ON THE YIELD AND QUALITY OF EARLY TURNIPS

1. RESPONSE TO DIFFERENT SUSTAINED SOIL MOISTURE REGIMES

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DESPITE recent increases in the use of irrigation in this country and the development of new techniques for measuring soil moisture status, little attention has been paid to the effects of different irrigation treatments on the yield and quality of vegetable crops.

This study was designed, therefore, to investigate the response of the early turnip crop to different degrees of depletion of the available soil moisture. It was stated by Theophrastus (*c.* 350 B.C. ; English trans., 1916) that the turnip plant (*Brassica rapa* L.) is extremely sensitive to depletion of soil moisture. Chittenden (1951) reports similarly but this has been confirmed by experiment only once and then with a variety of turnip grown as a leaf vegetable in the glasshouse (Hunter *et al.*, 1950). The latter found that plants watered when the soil moisture tension rose to 0·25 atmosphere gave significantly greater fresh and dry weights than those watered at 0·85 and 15·0 atmospheres.

Practical recommendations include those of Vilmorin (1904), who advised frequent irrigation to prevent any check to growth, and Smith (1954) who suggested that, if the land is irrigated before ploughing, a further application might be necessary when the plants are part-grown to enable the crop to finish successfully.

EXPERIMENTAL METHODS.

Soil moisture characteristics.

The turnip plants were grown in alluvial sandy loam overlying gravel at 30 inches. The water table was well below the greatest depth of rooting. The moisture characteristics of the root zone are shown graphically in Fig. 1, which indicates the amount of water needed to restore a given depth of soil to field capacity from any given soil moisture content. The graph was constructed from measurements made at 6-inch depth increments in the top 36 in. of the soil, field capacity being determined *in situ* (Veihmeyer and Hendrickson, 1931), permanent wilting point by the standard sunflower technique using soil samples (Veihmeyer and Hendrickson, 1945), and apparent specific gravity from the dry weight of soil cores taken from the sides of pits dug on the site. The data were combined to give the volume of available soil water according to the formula given by Israelson (1953).

The axis in Fig. 1, representing inches of soil moisture deficit, may be replaced by a time scale using the expected mean monthly soil moisture deficit calculated

from long-term meteorological records (Pearl, 1954) and by this substitution the soil moisture content of a given depth of soil can be estimated for a given date under average summer conditions. Using figures for South Warwickshire it was apparent that, under average conditions of rainfall and transpiration, at no time would less than half of the available soil moisture remain in the top 3 feet of a soil completely covered by transpiring vegetation.

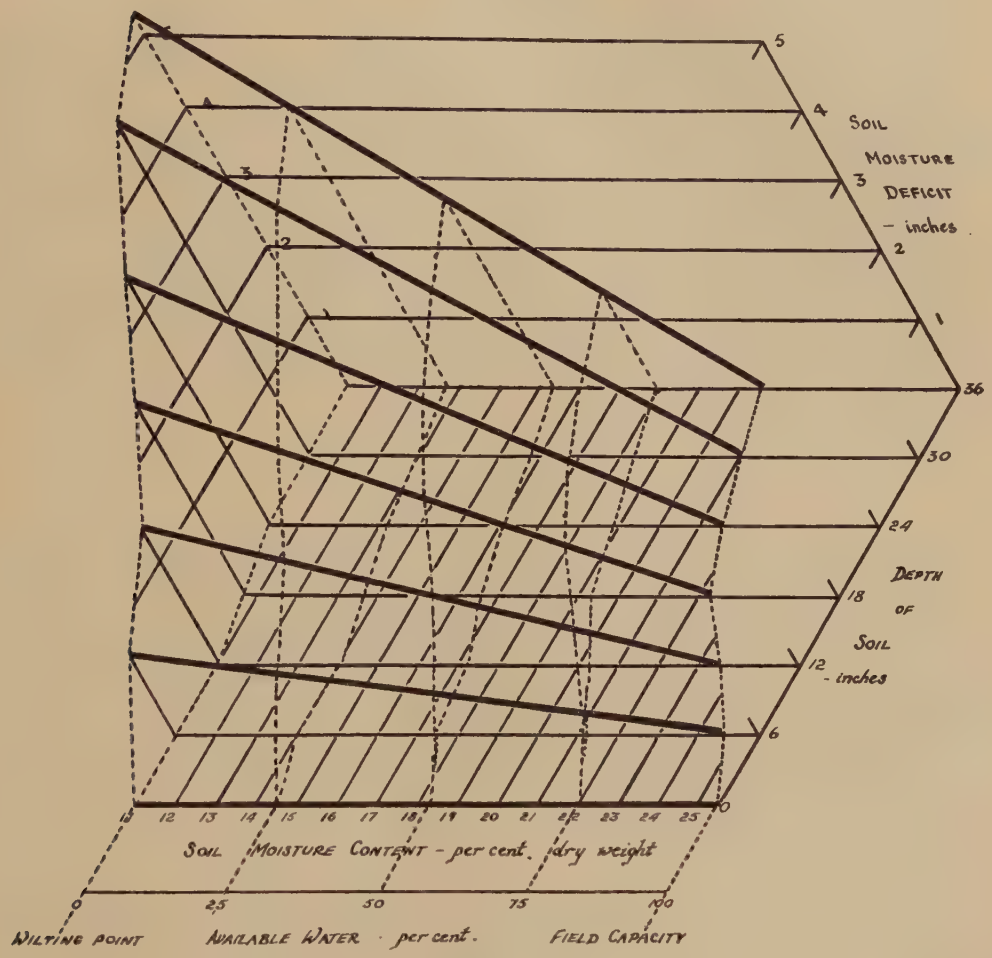

Fig. 1.

Soil moisture characteristics of the experimental site. This three-dimensional diagram was used to read off the number of inches of irrigation water needed to restore the root zone to field capacity (the soil moisture deficit) when the mean soil moisture content was known. It also enabled the average percentage of available water remaining in the soil to be read off by interpolation for different depths of soil once the soil moisture deficit had been estimated from meteorological data. For the sake of clarity, some intermediate points have been omitted.

Rain shelters.

In order to prevent rain from interfering with the treatments, mobile glass shelters, consisting of standard Dutch light frames bolted together at an angle of 120°, with wheels housed in the under side of the frames, were used to cover the plots when rain was falling during the day or when it was forecast that rain would probably fall during the night. The shelters moved on gutters, 15 in. above ground level, which also served to carry rain water off the plots.

Water application and amounts required.

The amount of water applied was measured by means of a rotary piston meter in the delivery line. The rate of flow was controlled by a trigger tap and the water was applied to the plots through a fine rose fitted to the outlet. The approximate soil moisture deficit was calculated on the basis of meteorological data and, when this approached the predetermined limiting soil moisture content, auger samples were taken to the full depth of rooting for gravimetric determinations of soil water. The depth of rooting was found by examining soil cores taken at 6-inch increments and the amount of water needed to restore the root zone to field capacity was then read off Fig. 1. The time needed for gravimetric determinations precluded the use of this method for deciding the daily water requirements of the plots receiving the wet treatment. With these the amount of water to be applied was obtained by calculating the evapo-transpiration during the preceding 24 hours, using local meteorological data and Penman's formula (1948).

Fibrous roots.

Root investigations during growth and at harvest were made by separating the fibrous roots from soil cores of 300 c.c. volume. A sharp-edged metal tube was used to obtain sample cores of soil at 6-inch depth increments and each soil core was placed separately in a cylindrical sieve made from 1 mm. copper mesh. Three such sieves were rotated by an electric motor in a 0·1 molar ammonia solution, the dispersed soil particles passing through the sieve and leaving the roots entangled on the central axle. The method took 5 minutes per core and was equally accurate with, and much quicker and less tiring than, the usual method of root determination by washing and hand separation. Coarse organic matter from the soil was removed by forceps before oven-drying the roots to a constant weight.

Treatments and cultural details.

Plots of spring-sown turnips, variety Early White Milan, were subjected to different soil moisture regimes by allowing the plants to deplete the available soil moisture within their root zone to three widely different points, viz. :

Treatment A. The soil in the root zone was rewetted to field capacity when wilting point was reached.

Treatment B. The soil in the root zone was rewetted to field capacity when 50 per cent. of the available water had been removed.

Treatment C. The soil in the root zone was rewetted to field capacity each day.

The mobile rain shelters were used on plots undergoing the above treatments and the layout consisted of four randomized blocks each containing three plots. Four additional plots were arranged in a row alongside the experiment, but were not protected from rain and received no additional watering (*Treatment D*). Results from these plots were not included in the statistical analysis.

Early in April 1955, seed was sown in drills 1 in. deep and 10 in. apart. Eighteen days after germination, when two true leaves had emerged, the plants were thinned to 9 in. apart in the rows. The soil in all the plots was then restored to field capacity by watering and the differential irrigation treatments were started.

Harvest measurements.

The crops were harvested 11 weeks after sowing when the turnips had reached marketable size. At harvest, the mean weight of edible roots and mean leaf number and area per plant were determined. The specific gravity of the edible roots was determined from their fresh weight and water displacement. The quality of the roots from the various treatments was assessed by a tasting panel which placed samples of cooked, diced roots in ranked order according to their strength of flavour, wateriness and fibrosity. The data were transformed for constancy of variance (Fisher and Yates, 1948) before statistical analyses were carried out.

An estimate of leaf area was obtained by using regression equations to relate fresh weight of leaf to leaf area and a separate regression for each plot was calculated from planimeter measurements made on a random sample of one hundred leaves.

EXPERIMENTAL RESULTS.

Soil moisture determinations.

The measurement of soil moisture content by oven-drying auger samples is subject to the variance inherent in any sampling technique, and the extent of this variance was estimated from a large number of soil samples taken at random in the area afterwards used for the experiment. The results show that the calculated standard error, when three replicate samples were used, was 2·7 per cent. of the mean value. Differences of 0·4 to 0·8 per cent. between the mean soil moisture contents of sets of three samples were found to be statistically significant ($P=0·05$), the difference required for significance being dependent on the actual soil moisture content. The variance did not differ significantly between the means of groups of samples taken from fallow and cropped areas, or between the means of samples taken from the top and second foot depth of soil.

Water application, total evapo-transpiration and efficiency of water use.

All plots had received 1·53 in. of rain before the experimental treatments were begun. The total evapo-transpiration during the life of the crop was calculated from soil moisture data taken at the time of sowing and of harvesting, and from the volume of water applied. The water-use ratio was calculated by dividing the total evapo-transpiration per plant, in grams, by the dry weight (gm.) per plant at harvest time. The data are set out in Table I.

TABLE I.

Effect of different water regimes on water application, water loss and efficiency of water use.

Treatment	A Dry regime	B Medium regime	C Wet regime	D Rain only
Water application (in.) ..	0	3·30	5·21	3·92
Number of applications ..	0	4	46	21
Total evapo-transpiration (in.)	4·2	4·5	5·2	4·6
Water-use ratio	328	278	282	—

Measurements of evapo-transpiration showed that plots which received the field-capacity treatment (C) lost 20 per cent. more water than plots that were never watered. There are two possible explanations for this. The transpiration rate may have been reduced by the lack of soil moisture in the dry plots or, alternatively, the frequent applications of water in the field-capacity treatment may have increased the water loss by direct evaporation from the wet soil surface. The second explanation is more likely and the increase in water loss would be accounted for by an increase in evaporation of 0·02 in. per day at each application of water.

The water-use ratio (water loss per unit of dry-weight gain) provides a valid method of comparing, within one experiment, the efficiency of different watering treatments in increasing plant growth. Here, the plants which received the intermediate treatment were more efficient in utilizing water than plants given either the wet or the dry treatment. In plots receiving the dry treatment the least amount of water was lost but this water was used less efficiently by the plants from the point of view of dry-weight gain.

The methods adopted for calculating the amount of water needed to rewet the soil of the root zone to field capacity were deemed satisfactory because samples taken after watering showed the soil to be at field capacity to the required depth. In the plots under the wet treatment, where the amount of water applied daily was equal to the calculated evapo-transpiration of the previous 24 hours, the soil moisture content was checked by weekly soil sampling. These soil samples showed that, at the times of sampling, the soil was at field capacity. Overwatering and consequent leaching would have been detected by soil sampling as the soil of the experimental plots does not drain down to field capacity until 48 hours after it has been overwatered. The results which were obtained indicated that the water loss had been calculated correctly within the limits of accuracy detectable by soil sampling.

Leaf growth.

The upper portion of Table II gives the data relating to leaves at the time of harvest. The total fresh weight was significantly reduced on plots in which more than 50 per cent. of the available water in the root zone had been depleted before rewetting (A), compared with plants from plots which were watered before this point had been reached (B and C). Leaf dry weight showed a similar response and differences in the water content of the leaves were small. The number of leaves was not affected by the different soil moisture regimes, a result similar to that obtained by Morton

and Watson (1948) with sugar beet. The proportion of plants with an inflorescence at harvest time (" bolters ") was similar under all treatments and there was no

TABLE II.

Effect of different water regimes on weight of leaves and weight and quality of edible roots.

Treatment	A Dry regime	B Medium regime	C Wet regime	D Rain* only	Sig. diff. P=0·01
Measurements of foliage					
Fresh weight of leaves (gm.)	189·3	252·5	259·0	235·9	21·5
Dry weight of leaves (gm.)	11·2	16·2	18·4	—	2·4
Number of leaves	17·8	17·2	17·9	17·8	1·2
Leaf area (sq. cm.)	3,010	3,522	3,593	—	309
Percentage of plants bolting	4·6	5·0	3·9	6·7	7·4
Measurements of edible roots					
Fresh weight (gm.)	85·2	110·9	136·8	165·4	22·9
Dry weight (gm.)	7·9	7·6	9·8	—	—
Specific gravity of edible root	0·95	0·95	0·95	0·97	0·17
Crude protein of edible root (per cent. dry weight)	21·7	20·3	18·7	—	2·3
Edible root quality (rank numbers)					
Strength of flavour	2·1	1·7	2·3	—	0·9
Wateriness	1·6	1·7	2·7	—	0·7
Smoothness of texture	2·1	1·5	2·5	—	0·8

* Results from plots which received treatment D cannot be compared statistically with those from the other three treatments.

evidence to support the view that dry soil conditions encouraged bolting (Chittenden, 1951). The effect of the three regimes on leaf area was similar to that on leaf fresh weight, although there was a clear indication that differences in the leaf area per unit leaf weight compensated for differences in total leaf weight per plant. A similar relationship was found with wheat plants by Watson (1937).

Root growth.

Differences in soil moisture status during the life of the crop had a greater effect on the yield of edible root than on leaf growth (Table II), and the fresh weight of the roots was significantly greater on plots maintained at field capacity by daily watering than under any other sheltered treatment. Yield of dry matter was higher in the wettest treatment but the differences were not statistically significant. No hollow roots were found in any treatment and the specific gravity of the roots was unaffected by differences in soil moisture.

The driest regime produced roots with the highest crude protein content. This supports previous findings that the percentage of nitrogen in the dry matter of the plant is increased by high soil moisture stress (Petrie *et al.*, 1943 ; Wadleigh and Ayers, 1945).

Edible root quality.

The results obtained in the tasting tests are summarized in the lower part of Table II. The numbers given are the means of the ranking values allotted by the tasting panel. High numbers indicate mild-flavoured, watery, smooth-textured roots and low numbers the opposite qualities.

Significant differences in the quality of roots were produced by the three treatments. The roots from plots which were given the field capacity treatment (C) had the smoothest texture and wettest flesh with the mildest flavour, although differences in flavour were not statistically significant. Smooth texture, succulent flesh and mild flavour are desirable qualities in root vegetables, but the majority of panel members described the roots from the field capacity treatment as " insipid " and " flavourless ".

Distribution of fibrous roots.

The histograms shown in Fig. 2 were drawn from data obtained by the core sampling and root separation method previously described. Each value is based on the mean of results from eight soil cores at each depth.

Fig. 2 shows that the treatments altered the total amount of fibrous roots at harvest as well as the pattern of distribution. The driest treatment produced the deepest root system whereas plants from plots under the wet regime had the majority of their roots in the top 6 inches. It is noteworthy also that the driest treatment did not markedly reduce the total weight of fibrous roots although this treatment caused a reduction in the yield of leaves and of edible roots (Table II). The smallest total weight of fibrous roots was produced by plants receiving the intermediate treatment where intermittent applications of water apparently imposed a greater check to fibrous root growth than the gradually drying soil conditions of treatment A.

Examination of the data from soil samples showed no correlation between the rate of water depletion and the amount of fibrous roots at any given depth within the root zone, and the data showed a remarkably even pattern of soil moisture extraction throughout the root zone. Small differences were eliminated by converting the soil moisture content to a percentage of the available water within the corresponding soil horizon. When expressed in this manner, the moisture content of soil samples taken at any depth within the root zone was always within 5 per cent. of the mean value for the whole root zone. This suggests that the water requirements of the turnip plant can be satisfied by a small proportion of the total fibrous root system and that, under normal conditions, the root system as a whole functions considerably below its maximum possible rate of absorption. This result supports the views of Rosene (1955) who calculated, from micropotometer root investigations, that the water loss from a mature rye crop during a bright summer's day could be met by the root system absorbing water at 2 per cent. of its maximum rate of uptake.

Rain shelters.

The rain shelters were in place over the crop for 14 per cent. of its life and for 22 per cent. of the daylight hours.

The mean weight per plant from the unsheltered plots (Treatment D of Table II), which received rainfall only, was 16 per cent. heavier than the general mean weight

of plants from the 12 plots sheltered from rain and was equal to the highest yielding treatment which was sheltered.

Measurements showed that the shelters, even when continuously in position, reduced the diurnal temperature range at crop level by only 1° F., while the mean daily temperature was unaffected. However, they reduced light intensity at crop canopy level by 40 per cent. as measured with a selenium photocell and this probably caused the observed depression in growth.

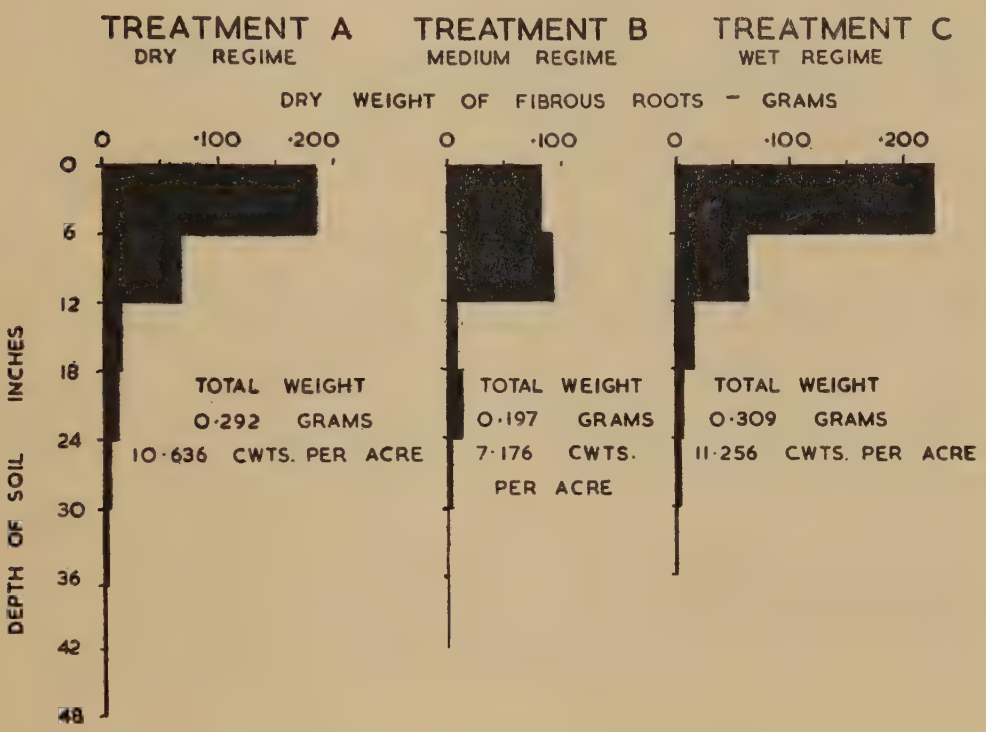

Fig. 2.
Distribution of fibrous root system.

Blackman (1953) has shown, with a number of field crops, that reduction in light intensity during the summer reduced growth as a result of a decrease in the net assimilation rate, despite a compensating increase in the leaf area of the shaded plants. Comparisons of the ratios of leaf to root weights of plants from the sheltered and unsheltered plots agreed with this finding and supported the view that the depressant effect of the rain shelters on yield was caused by the reduction in illumination. The wet and medium regimes (Treatments B and C), which were protected by covers, produced a greater leaf weight than the unsheltered plants (Table II), but despite this they produced a smaller weight of edible root, presumably because of lowered net assimilation rate of the leaves.

Thus absolute yields obtained in this experiment where rain shelters have been used are not directly comparable with those to be expected in the absence of shelters. Nevertheless, there is no reason to suppose that the results of comparisons made under sheltered conditions would not apply to crops grown in the open.

DISCUSSION.

The results of the present experiment do not agree with the views of Veihmeyer and Hendrickson (1950) who concluded, after a review of much experimental evidence, that soil water is equally available to plants for growth at all moisture contents between field capacity and permanent wilting point. In this experiment the yield both of leaves and of edible roots at harvest was reduced when the soil moisture content was allowed to fall below field capacity. This agrees with the result obtained by Hunter *et al.* (1950). Other workers (Frei, 1954 ; Salter, 1954) have also found that the growth of plants was checked if soil moisture status was allowed to fall below field capacity. It has been suggested by Hudson *et al.* (1957) that plant growth may not be affected by differences in available soil moisture content in the zone of soil first occupied by roots, so long as other roots are growing into soil at field capacity. They cite in support of this the different responses of tomato and lettuce plants growing under similar conditions and subjected to the same four soil moisture regimes. Tomatoes responded to the different treatments once their roots had penetrated the full depth of soil available but did not do so until that stage had been reached. On the other hand lettuce plants, which were harvested before this stage was reached, showed no response to the different soil moisture regimes. This explanation does not fit the results obtained in the present experiment where the depth of the root zone of the turnip plants was increasing regularly at the rate of half an inch per day up to the time of harvest. Half an inch depth of the soil used in this experiment contained 0·07 in. of available water, which was sufficient to satisfy the average daily water loss. Despite this, the growth rate was affected by different soil moisture regimes, suggesting that, in the turnip, soil moisture uptake from the zone of root extension was not sufficient for maximum growth.

SUMMARY.

1. Turnip plants, variety Early White Milan, growing in the field, were subjected to three soil moisture regimes controlled according to the results of regular soil moisture determinations and Penman's meteorological method. Mobile glass shelters were used to prevent rain from interfering with the treatments.

2. The use of the rain shelters resulted in a lower growth rate which was probably caused by the reduction in light intensity under the shelters.

3. Plots maintained at field capacity by daily watering gave the greatest fresh and dry weights of edible root and leaf material at harvest. The yield of edible roots was markedly reduced when watering was delayed until 50 per cent. of the available water of the root zone had been lost. Leaf area and the weight and distribution of the fibrous roots were also influenced by the soil moisture regimes.

4. The quality of cooked roots was affected by the soil moisture status under which they were grown. Roots from the plots maintained at field capacity had less

flavour, more watery flesh and a smoother texture than roots from plots which received the drier treatments.

5. Total evapo-transpiration was greater from plots kept at field capacity. This was attributed to the greater loss of water by direct evaporation from the wet soil surface. The weight of water lost, per unit weight of dry matter produced, was greatest in plants from plots given the intermediate watering treatment.

ACKNOWLEDGMENTS.

The experiment described formed part of the work carried out at the National Vegetable Research Station, Wellesbourne, during the tenure of a Ministry of Agriculture Scholarship, and provided part of the material of a thesis submitted for the degree of Doctor of Philosophy of Reading University. Grateful thanks are due to the Ministry of Agriculture, to the National Vegetable Research Station for providing facilities and to Mr. E. J. Winter for his help and advice at all stages of the work.

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(*Received* 20/6/57.)

THE EFFECTS OF WINTER CHILLING ON THE SUBSEQUENT GROWTH AND DEVELOPMENT OF THE CULTIVATED STRAWBERRY PLANT

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THE summer-fruiting varieties of strawberry grown in the open in Britain generally initiate flower trusses in late summer and autumn, but under comparable temperature and daylength conditions in spring no flower trusses are formed. Observations on several summer-fruiting varieties (Robertson and Wood, 1954, and Guttridge, 1955) have confirmed previous observations of van den Muijzenberg (1942) and several American workers, and it is now well established that flower initiation does not take place in spring in the northern states of U.S.A. or in northern Europe. A similar situation arises in the American everbearing varieties (Waldo, 1930) and in French perpetuals grown at Mylnefield.

It seems likely that the absence of flower initiation in spring results from changes in the plant brought about by low temperatures in winter. Experiments were set up to test this and to give a critical appraisal of the differences between growth in autumn and growth in spring. Comparisons were made by growing the plants at each of these seasons in a controlled environment.

Facilities for growing plants in controlled environments.

The facilities at the Horticultural Laboratories of Reading University (Vince *et al.*, 1956) were used for the first experiment in the winter of 1952–3. In the winter of 1954–5 a second experiment was carried out at Mylnefield in growth rooms which have been briefly described in the Scottish Horticultural Research Institute Annual Report for 1954–5.

At Reading the controlled environment cubicle was adapted by fitting two 400-watt H.P.M.V. (MA/H) lamps, one 500-watt Sieray Dual (MAT/V) lamp of which some 275 watts are mercury discharge and 225 tungsten incandescent light, and two 80-watt " Daylight " fluorescent lamps. This combination of lamps gave a mean light intensity over the whole bench area of 316 f.c. as measured by a G.E.C. General Purpose Illumination Meter. The photoperiod was 12 hours. There was a diurnal temperature variation of about 8° F. The mean temperatures, calculated from thermograph traces, for the three batches of plants grown in the cubicle at different times were 59·7° F., 59·8° F. and 60·0° F.

At Mylnefield two growth rooms were available, the second only for part of the experiment. In the first room, light was provided at a mean intensity of 830 f.c. by seventeen 80-watt " Northlight " fluorescent lamps, four 40-watt and eight 25-watt incandescent lamps, all suspended 36 in. above the bench. These conditions are later referred to as the " high light " environment. The second growth room was illuminated by twelve 80-watt " Northlight " lamps and four 40-watt and eight

15-watt incandescent lamps suspended at the same height above the plants, giving a mean intensity of 513 f.c. This provided a " low light " environment which was available for the after-chilling treatments only. Intensities are means of 60 readings taken equidistantly over the bench areas with an E.E.L. photometer held horizontally 8 in. above the bench. The temperature in both rooms was thermostatically controlled at 60–62° F. The photoperiod was 11 hours. The humidity was not accurately controlled at either centre. At Mylnefield hygrograph records indicated that the relative humidity varied between 65 and 85 per cent. with the lamps on, and 75 and 95 per cent. with the lamps off. The positions of pots containing the plants were regularly changed to equate positional effects.

Experiment 1. Reading, 1952–3.

Young plants of the varieties Royal Sovereign and Auchincruive Climax, well established in 6 in. clay pots, were randomly divided into two groups on 6th October. One group was immediately brought into a heated glasshouse and grown under a long photoperiod until 4th December, a treatment calculated to inhibit the onset of dormancy. This group is described as " partially dormant " as the subsequent growth of the plants suggested they were in this condition. The second group was left outdoors until 7th November when, to avoid subjecting the plants to low temperatures likely to break dormancy, they were brought into an unheated glasshouse until 4th December. These plants received the natural short photoperiod throughout the autumn and, to judge by their subsequent growth, they became dormant. On 4th December each of the two groups of plants was divided into three sub-groups for cold storage treatment. The first of these received no cold storage, the second received 36 days and the third 72 days of cold storage at 35–40° F. Two 40-watt " Daylight " fluorescent lamps provided low intensity illumination in the cold store for 8 hours daily. The cold treatment resulted in slight marginal necrosis of the leaves of " partially dormant " plants ; the dormant plants appeared undamaged.

After the appropriate cold treatment the plants were transferred to the controlled environment cubicle. The first sub-group was therefore transferred directly to the cubicle on 4th December, the second 36 days later and the last after a further 36 days. To check the efficacy of the cold storage treatments 7 dormant Sovereign and 7 dormant Climax plants were returned outdoors on 4th December to receive the natural cold temperatures of the season until being placed in the cubicle 72 days later. There were 7 plants of each variety in each treatment.

Records of growth were made every 18 days, and on these occasions all stolons, branch crowns and inflorescences were removed. Initially plants of all treatments grew well, but after a month or so, depending on treatment, epinasty of the leaf margins and marginal yellowing occurred in some Sovereign plants. No such symptoms were observed in the Mylnefield experiment, and it seems possible that they may have been induced by light from the H.P.M.V. lamps.

The results are presented in Table I. Flower initiation was delayed appreciably in Sovereign only, following cold storage for both 36 and 72 days (Table I, A). Stolons were formed in Sovereign after 72 days cold storage (Table I, B). The rate of leaf production (Table I, C) during the first 36 days in the cubicle increased with the length of cold storage. During the second 36-day period the rate of leaf produc-

Table I.

Data from Experiment 1, Reading, 1952–3.

		Sovereign, autumn treatment		Climax, autumn treatment	
		Outdoors (dormant)	In glasshouse (partially dormant)	Outdoors (dormant)	In glasshouse (partially dormant)
A. Mean no. of leaves initiated before inflorescence initiation*	No cold	0·6	1·4	2·8	2·6
	36 days cold	3·7	1·5	2·5	2·0†
	72 days cold	5·8	3·0†	3·2	2·7
B. No. of stolons formed	No cold	0	0	0	0
	36 days cold	0	0	0	0
	72 days cold	9	1	0	0
C. Mean no. of leaves emerged during first period of 36 days in the controlled environment	No cold	3·9	3·6	3·2	3·0
	36 days cold	4·5	4·1	3·6	2·8
	72 days cold	5·2	4·3	4·6	3·7
D. Mean petiole lengths (mm.), measured when fully extended, of leaves emerging on the 18th, 36th and 54th day after the plants were put into the cubicle	No cold	97·1	86·8	46·2	53·3
	36 days cold	131·4	109·7	67·8	54·9
	72 days cold	155·5	140·0	101·0	80·1

* Number of leaves emerging before the inflorescence, less the mean number of leaves in the bud estimated by dissecting a sample of 7 plants before growth in the cubicle.

† Mean of 6. One plant failed to flower.

tion showed no definite treatment differences. The figures of petiole lengths (Table I, D) show clearly the quantitative aspect of cold storage treatment. Seventy-two days cold storage had an appreciably greater effect than 36 days.

The initial growth in the cubicle of plants which had overwintered outdoors suggested that the 72 days of cold storage had not produced the maximum chilling effect. Growth records were, however, not obtained as these plants showed symptoms of severe frost damage.

Cold storage produced a greater effect in Sovereign than in Climax and the dormant series grew with rather more vigour than the partially dormant series. Root sections made after 72 days cold storage showed that plants of the dormant series had greater reserves of starch, which probably accounts for the latter difference.

Experiment 2. Mylnefield, 1954–5.

Plants from virus-free stocks of Royal Sovereign and Auchincruive Climax were raised in pots as before. Half of them were grown from 17th September to 17th November under steel wire-mesh shade screens which reduced the light intensity to about 15 per cent. of daylight. The remaining plants were grown in full daylight during the same period. Sampling showed that the shaded plants had a dry weight (root and crown) about two-thirds that of the non-shaded ones. Iodine tests showed a reduction in starch due to shading, indicating that the total starch reserve was reduced to less than two-thirds.

Plants for chilling were overwintered outdoors, exposed to the natural low temperatures. The mean of maximum and minimum screen temperatures during this period were : part of November, 42·5° F. ; December, 40·7° F. ; January, 34·1° F. ; February, 32·1° F. ; part of March, 36° F.

The dormant plants, both those shaded and those not shaded in autumn, were grown in the Mylnefield growth room for 12 weeks from 18th November. They had been subjected to little or no chilling. Sample plants were taken for bud dissection and dry-weight determination at the beginning (before growth) and end (after growth) of this period. Chilled plants, shaded or not shaded in autumn and then overwintered outdoors, were grown in the same growth room for 12 weeks as from 9th March, and plants were sampled as before. Similar plants were grown in the second (low light intensity) growth room in spring only.

There were 10 plants of each variety in each treatment. Growth was recorded at fortnightly intervals, when stolons, branch crowns and inflorescences were removed.

Very slight symptoms of frost damage were observed in the chilled plants but the effects are not apparent in the growth records.

Leaf growth outdoors during the period 18th November to 9th March was less than half a leaf per plant.

Dissection of sample plants on 18th November and 9th March showed in Sovereign a decrease in the mean number of leaves in the bud from 7·21 in November to 7·07 in March, a non-significant difference. In Climax the mean number of leaves in the bud increased significantly ($P=0·05$) from 6·94 in November to 7·50 in March.

The numbers of leaves initiated in the growth rooms before the inflorescence are given in Table II. There are highly significant differences between plants of the dormant and chilled series of both varieties in both shaded and non-shaded treat-

ments. Clearly flower initiation takes place much less readily in chilled plants. The differences between the dormant and chilled series are greater in Sovereign than in Climax. The effects of different light intensities on the chilled plants and also of shading and non-shading treatments in autumn are of a much lower order than the chilling effect and are either not or only just statistically significant.

TABLE II.

Mean number of leaves initiated per plant on the main axis before inflorescence initiation; Experiment 2.

	Sovereign, autumn treatment		Climax, autumn treatment	
	Not shaded	Shaded	Not shaded	Shaded
Dormant plants, high light	1·21	1·47	1·65	0·97
Chilled plants, high light	8·10	7·07	4·15	3·45
Chilled plants, low light	7·30	5·87	3·75	4·55

S.E. for comparisons between high light treatments=0·43.
S.E. for comparisons between chilled series=0·51.

TABLE III.

Mean number of stolons produced per plant; Experiment 2.

	Sovereign, autumn treatment		Climax, autumn treatment	
	Not shaded	Shaded	Not shaded	Shaded
Dormant plants, high light	0	0	0	0
Chilled plants, high light	3·9	3·1	3·8	3·7
Chilled plants, low light	3·3	1·1	3·6	3·5

The marked change in growth habit resulting from winter chilling is clearly shown by the stolon production (Table III). No stolons were formed by the dormant plants in contrast to the considerable stolon production of the chilled plants. Stolons were produced (although only a mean of 1·1 per plant) by autumn-shaded Sovereign plants in the low-light environment in spring, although this low light intensity barely supported growth of these Sovereign plants. Two of them in fact died. This is the only treatment that differs significantly from other spring treatments. Climax plants were less severely affected by this unfavourable combination of treatments.

During the first fortnight in the growth rooms the mean plastochron (time interval between emergence of successive leaves on a crown) for all chilled plants was 4·01 days, which is significantly different from the mean plastochron of 7·87 days for dormant plants. The initial high rate of leaf production in spring was probably not associated with a rate of leaf initiation of commensurate dimensions, as a temporary reduction in the number of developing leaves in the bud in spring has been observed

by Arney (1953). The mean plastochron for leaf emergence for subsequent fortnights was slightly longer in plants of the chilled series (9·33 days) than with the dormant series (8·59 days). This may have been associated with a partial recovery in the number of leaves in the bud in the chilled plants.

The petiole lengths are shown in Fig. 1. The differences between the dormant

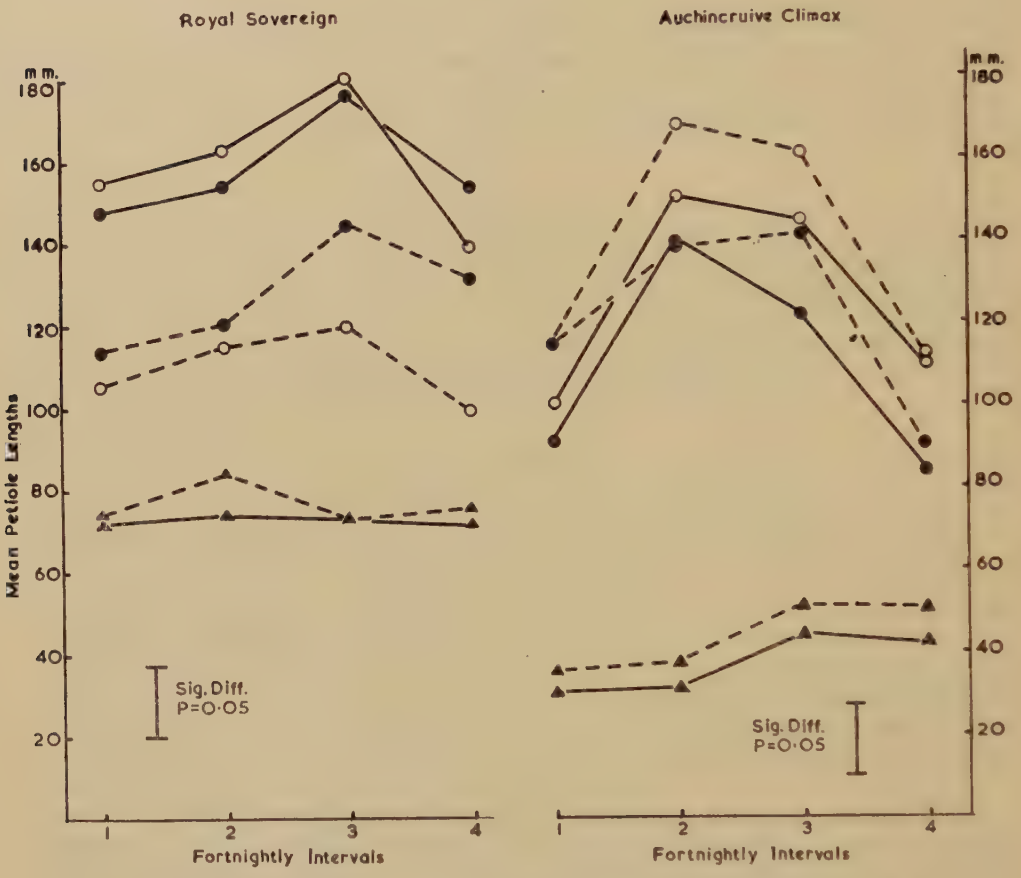

Fig 1.

Mean petiole lengths of leaves emerging at fortnightly intervals.

and chilled plants are clearly significant. The general weakness in Sovereign resulting from autumn shading, especially under the low light intensity treatment in spring, is apparent. In the stronger-growing Climax the low light intensity gave slightly etiolated petioles. The short photoperiod eventually resulted in a shortening of the petioles of both varieties in the fourth fortnight.

Figs. 2 and 3 respectively show dormant and chilled plants after equivalent periods of time in the growth rooms. In addition to the recorded differences in growth the photographs also show that leaf size is greater after chilling.

The dry-weight measurements of root+crown (stem but not leaves) of sample plants, both before and after growth in the growth rooms, show (Table IV) a consistent pattern of variation, apart from the figure underlined in Table IV. With this one exception, there is little difference in the before-growth samples taken in November and those taken in March. The before-growth and after-growth figures for the dormant series show that there was an increase in dry weight of roots and crowns during the 12-week period in the growth rooms. In the chilled series, in a similar 12-week period, dry weights decreased, presumably with the utilization of food reserves. This decrease was greater under low light intensity. The mean increase in plants of the dormant series is significantly different from the decreases in plants of both chilled series. No explanation can be given for the underlined figure and a technical error is assumed.

TABLE IV.

Mean dry weight (gm.) of root+crown per plant; Experiment 2.

		Sovereign, autumn treatment		Climax, autumn treatment		Mean*
		Not shaded	Shaded	Not shaded	Shaded	
Dormant plants, high light intensity	Before growth	8·7	5·3	20·2	13·7	
	After growth	12·0	6·8	20·9	15·6	
	Increase	3·3	1·5	0·7	1·9	1·85
Chilled plants, high light intensity	Before growth	8·7	5·1	19·5	9·8	
	After growth	8·3	5·0	15·2	12·5	
	Increase	−0·4	−0·1	−4·3		−1·60
Chilled plants, low light intensity	After growth	6·8	4·9	14·2	11·8	
	Increase	−1·9	−0·2	−5·3		−2·47

* 7–12 plants.
S.E. for comparison of mean increases = 0·854 gm.

DISCUSSION.

The experiments demonstrate that a major physiological change takes place in the strawberry varieties Royal Sovereign and Auchincruive Climax during the winter. That this change is brought about by low temperatures is indicated by the results of the Reading experiment. Increasing length of cold treatment up to 72 days at 35–40° F. led to increasing change in the plants. The early vigour shown by the plants which were overwintered outdoors at Reading, but which were damaged by frost, suggests that the chilling requirement was not fully satisfied by the cold storage treatment. The low level of vegetative vigour of Climax plants after chilling at Reading suggests that this variety has a greater chilling requirement than Sovereign. The natural winter cold treatment at Mylnefield was highly effective.

In the Reading experiment the difference in growth between the dormant and partially dormant series after chilling may have been due to differences in food reserves and not to different effects of chilling on dormant and partially dormant plants. The Mylnefield results indicate that small differences in growth can be induced nutritionally.

The differences in vegetative vigour at Mylnefield induced by treatments designed to affect the carbohydrate nutrition were much smaller in both varieties than differences induced by chilling. The combined treatments of autumn shading and low light intensity in the growth room, although resulting in the death of two Sovereign plants, still permitted a clear expression of the effects of chilling. There is no evidence here to suggest that the reduced carbohydrate reserves of the autumn-shaded treatment affected the results in any way other than by restricting the full expression of post-chilling vigour as did the low light intensity treatments.

Further evidence that the vegetative growth observed in the field in spring is due to a physiological condition of the plants, rather than to any special features of the spring climate, is provided by the results of another experiment at Mylnefield. Plants of four varieties, including Sovereign and Climax, cold stored from March and planted in September in the field, failed to initiate flowers during the autumn, indicating that they had retained their post-chilling physiological condition.

The characteristics of growth of dormant plants under short photoperiods in these experiments were short petioles, production of branched crowns rather than of stolons, continued flower initiation as suitable apices became available and increased dry weight of root and crown. In spring, after chilling, growth under short photoperiods was characterized by an initial high rate of leaf emergence, long petioles, larger leaves, stolon production, delayed flower initiation, and decreasing root and crown dry weight, probably as the result of utilization of food reserves for top growth. In the spring, growth is potentially vegetative ; in the autumn, it is potentially reproductive.

The present experiments support the suggestion of an annual cycle of physiological condition in cultivated strawberry plants. The annual development in the field results from the integration of this and the seasonal climatic cycle.

SUMMARY.

Two experiments were carried out to investigate the influence of low temperatures in winter on the subsequent growth of two cultivated strawberry varieties, Royal Sovereign and Auchincruive Climax.

In the first experiment chilling treatment was given in a cold store at 35–40° F. Plants subjected to no chilling, 36 days and 72 days of cold storage, were grown independently in a constant environment cubicle. In the second experiment plants were exposed to low winter temperatures outdoors. Batches of plants were grown in the growth rooms both in November (having had little or no chilling) and in March (after chilling).

The results show that low temperatures in winter have a marked effect on the subsequent growth of the plants. Plants placed in November under the controlled conditions of an eleven-hour photoperiod at 60–62° F. continued flower initiation, produced no stolons, had short petioles, small leaves, and increased root and crown

PLATE I

Fig. 2.

Auchincruive Climax plant (left) and Royal Sovereign plant (right) of the dormant series after 10 weeks in the high light intensity growth room. These plants received full daylight in autumn. Experiment 2.

Fig. 3.

Auchincruive Climax plant (left) and Royal Sovereign plant (right) of the chilled series after 10 weeks in the same growth room. These plants received full daylight in autumn. Experiment 2.

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dry weight. After subjection to low temperatures, similar plants under a similar environment made vigorous vegetative growth with strong runner production, long petioles and large leaves, while flower initiation was delayed for several weeks.

Modification of the carbohydrate status by shading in autumn and by low light intensity treatments in spring had a small effect on the expression of post-chilling vegetative vigour.

ACKNOWLEDGMENTS.

The author wishes to express his thanks to Professor R. H. Stoughton, under whose supervision the first part of this work was carried out at Reading University, and to colleagues at Mylnefield for help with the preparation of this paper.

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(*Received* 25/6/57.)

THE CONCENTRATIONS OF CERTAIN NUTRIENT ELEMENTS IN APPLE LEAVES TAKEN FROM DIFFERENT POSITIONS ON THE SHOOT AND AT DIFFERENT DATES THROUGH THE GROWING SEASON

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East Malling Research Station, Kent

Workers engaged on the problem of interpreting leaf analysis data for assessing the nutritional requirements of fruit trees are well aware that the concentrations of various mineral nutrients found in leaves are dependent on the position of the leaf on the shoot, the type of shoot and the time of year at which the sample is taken.

The only systematic studies of the variation in percentage composition of leaves of apple plants which have been published relate to the seasonal variation for a given leaf position on the shoot (e.g. Cain and Boynton, 1948 ; Rogers, Batjer and Thompson, 1953 ; Emmert, 1954) or to the variation in concentration in successive leaves on the shoot on one particular occasion, as, for example, the work of Kidson (1947) on potassium and magnesium. Roach *et al.* (1957) show by means of a series of diagrams how the concentrations of potassium, iron and manganese vary in successive leaves of M.VII rootstocks when grown in spray culture solutions deficient in these elements, but such data have a rather specialized interest.

In the investigation of leaf analysis problems it is clearly desirable to have a good idea of the range of concentrations of at least the elements N, P, K, Ca, Mg, Fe and Mn to be expected in normal non-deficient leaves when sampled in various ways and at different times. Hence an experiment was carried out on shoots from apple rootstocks growing in a stoolbed row. This type of plant material was chosen in preference to extension shoots on mature trees because it offered large numbers of the uniform shoots which were required. It seemed probable that leaves from these shoots would vary in the same way as leaves from vigorous young trees in the orchard, so that, while the information obtained might not be strictly applicable to other specific cases, it should at least make possible general comparisons of the information yielded by the various kinds of leaf sample used by different workers.

Experimental procedure.

Samples were collected from average length shoots of M.VII apple rootstocks which were growing in a 300 ft. stoolbed row and which, by the end of the season, had reached a height of about 2½ ft. It was not possible to count the leaf number from the first node upwards as stoolbed shoots are earthed up. The following system of numbering was therefore adopted.

For each sampling the first unfurled leaflet near the stem apex was numbered " 1 ", then leaf numbers were counted downwards from this as far as the seventh

leaf. The position of the lowest leaf on the earthed-up shoot was designated " B " and the leaf midway between it and the apex was labelled " M ". Leaf positions counted upwards from leaf B were distinguished by a minus sign : thus the leaf 2 nodes above B was labelled " (—2) " and that 4 nodes above B was " (—4) ", and so on.

From twelve to thirty-six leaves, according to their size, were collected from each of the positions 1 to 7, M, (—4), (—2) and B at each sampling, except in the early part of the season when the shoots were short and fewer sampling positions were available. For each position one leaf was detached from each of the required number of shoots of average length chosen at random. The interval between samplings was usually 14 days.

The leaves were washed first in water containing 0·2 per cent. of " Teepol " and then in distilled water, dried at 80° C. and ground by hand in an agate mortar. The dried material was analysed chemically by the following methods : nitrogen by semi-micro Kjeldahl, phosphorus by the molybdo-vanadate reagent, potassium by the silver cobaltinitrite reagent, calcium by Mason's method (1952), magnesium by the Titan Yellow reagent, iron by 2:2′-dipyridyl and manganese by tetramethyl-diaminodiphenyl methane.

RESULTS AND DISCUSSION.

The results of the investigation are presented graphically in Figs. 1 to 7, each of which is divided into fourteen sub-diagrams which correspond with the sampling dates. Attention is drawn to the fact that, with a few exceptions, the B position on any one sub-diagram overlaps position 1 on the next. In the first three sub-diagrams there were no separate M–position samples but the position of the middle leaf is marked by an arrow.

The analytical results obtained were compared with those from a similar but less ambitious experiment, made in the preceding year, the samples being taken at monthly intervals. The comparison suggested that differences in leaf composition due to weather conditions and the site on which the material was grown were, at all events in these two experiments, relatively unimportant and exerted only a minor effect on the distribution patterns of the various elements. Data for the second experiment only are given in this paper.

Sub-diagrams 1 to 7 show that a relatively orderly change occurs in the concentrations of elements during the period of extension growth which ceased about the middle of August ; and sub-diagrams 8 to 14, excluding 11, show how mere ageing, as distinct from extension growth, affects the concentrations of elements in successive leaves on the shoot. Sub-diagram 11 differs sharply from those on either side of it and this calls for some comment. When the normal fortnightly sample was being taken on 24th September 1952, it was noticed that a number of shoots in the stoolbed had resumed apical growth. These shoots were sampled on the following day in order to determine the effect of extension growth so late in the season. It will be noted that in general sub-diagram 11 resembles No. 7, where extension growth was still in process, rather than No. 10. Comparison of sub-diagrams 10 and 11 suggests that high concentrations of phosphorus and potassium and low concentrations of calcium, magnesium and manganese are associated with expanding leaves. The effect of renewed growth on nitrogen and iron concentrations is relatively small.

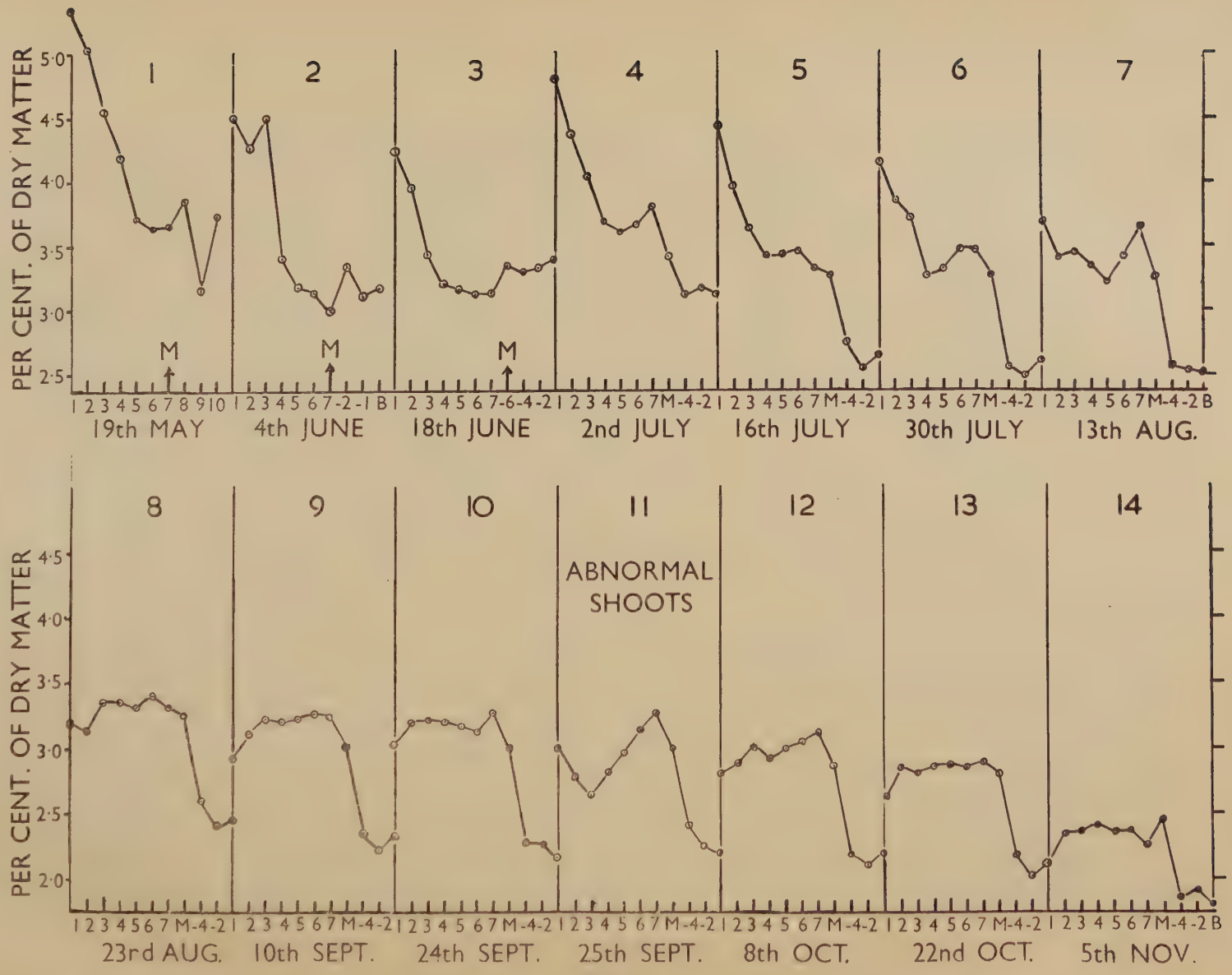

FIG. 1.

NITROGEN. Concentration of the element in the dry matter of leaves of apple shoots (from stoolbeds) between 19th May and 5th November. Leaf positions are numbered from the apex, which is to the left of each sub-diagram. M refers to the mid-shoot leaf and B to the leaf nearest the base.

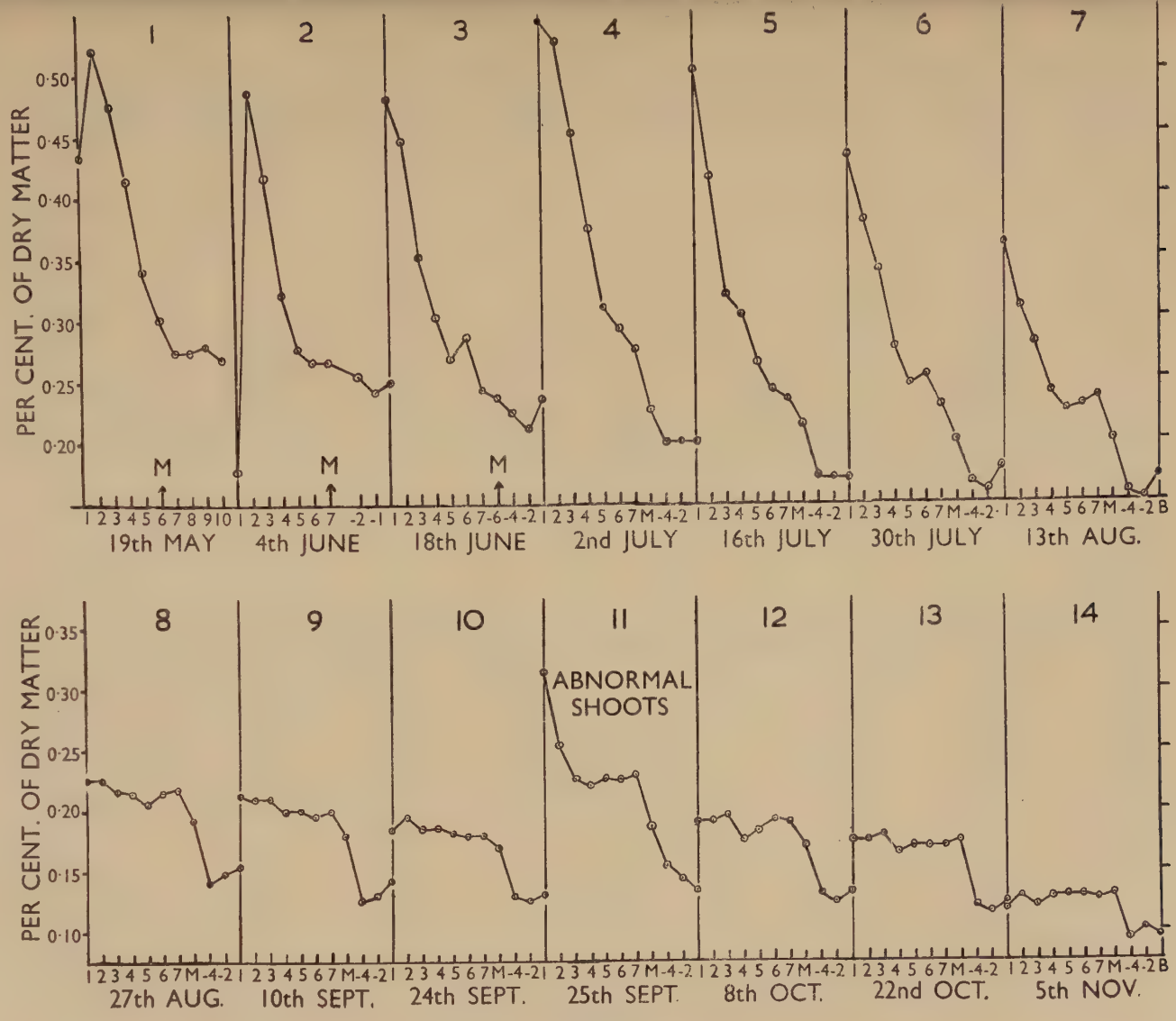

FIG. 2.

PHOSPHORUS. See legend under Fig. 1.

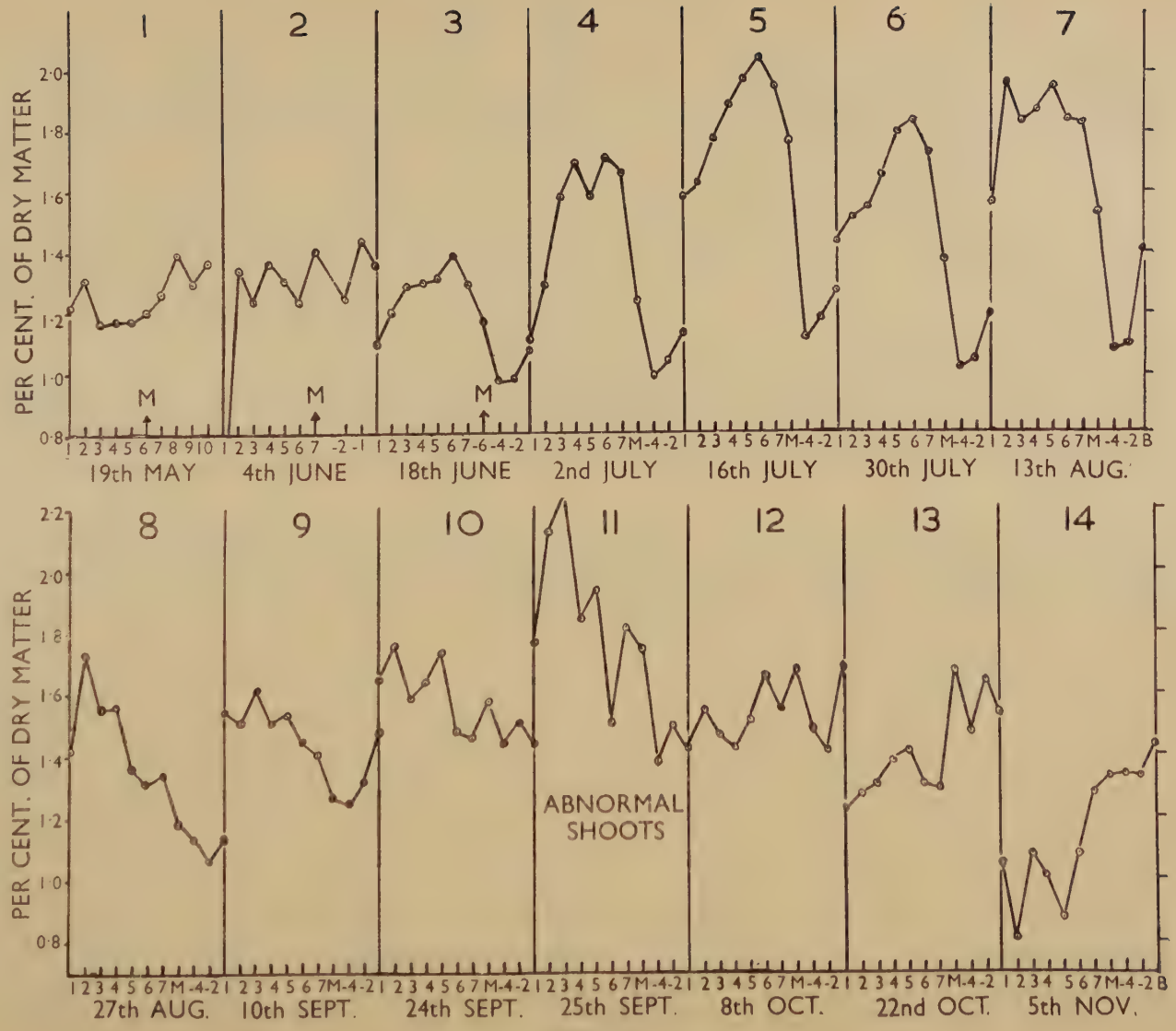

FIG. 3.

POTASSIUM. See legend under Fig. 1.

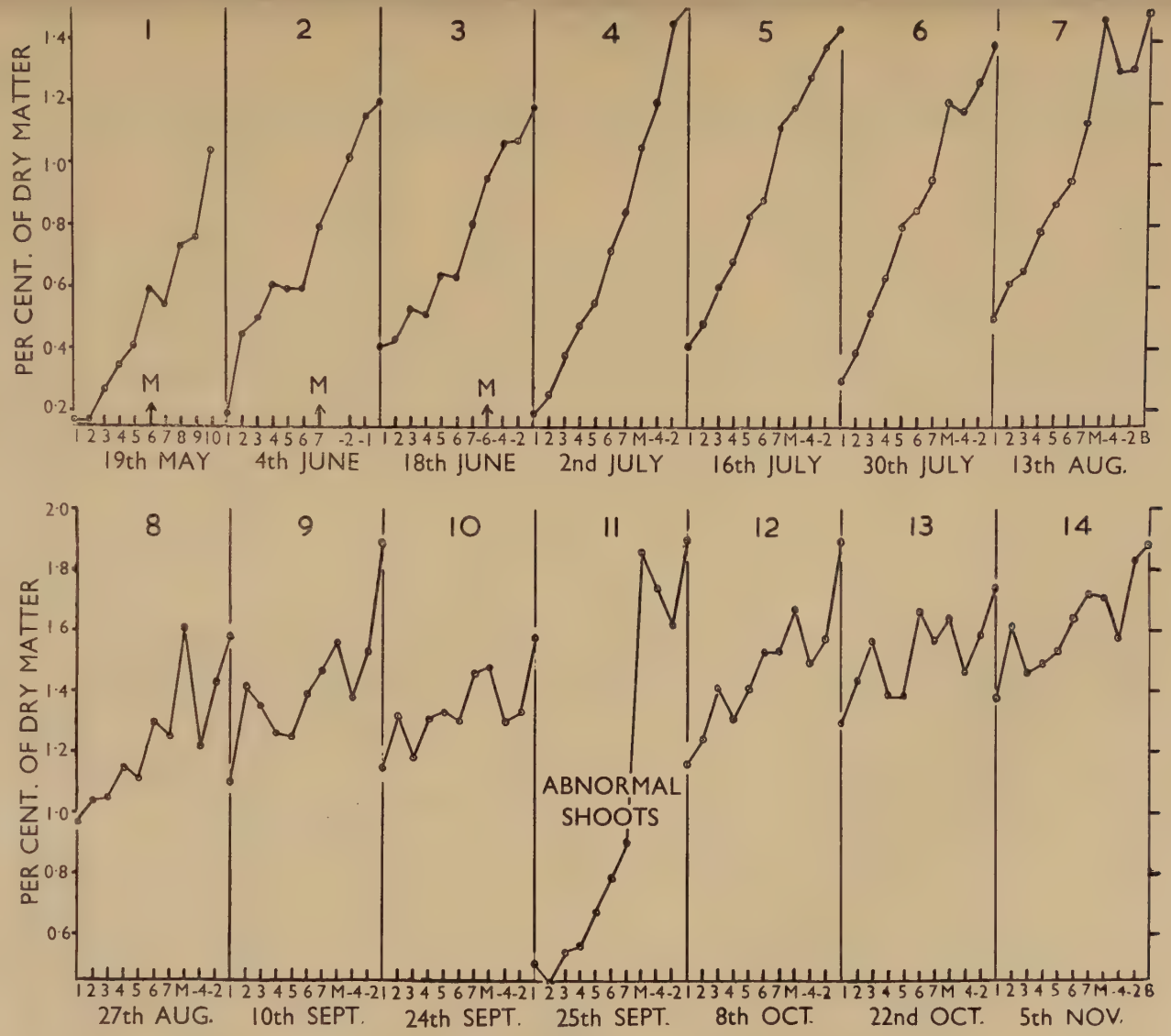

FIG. 4.

CALCIUM. See legend under Fig. 1.

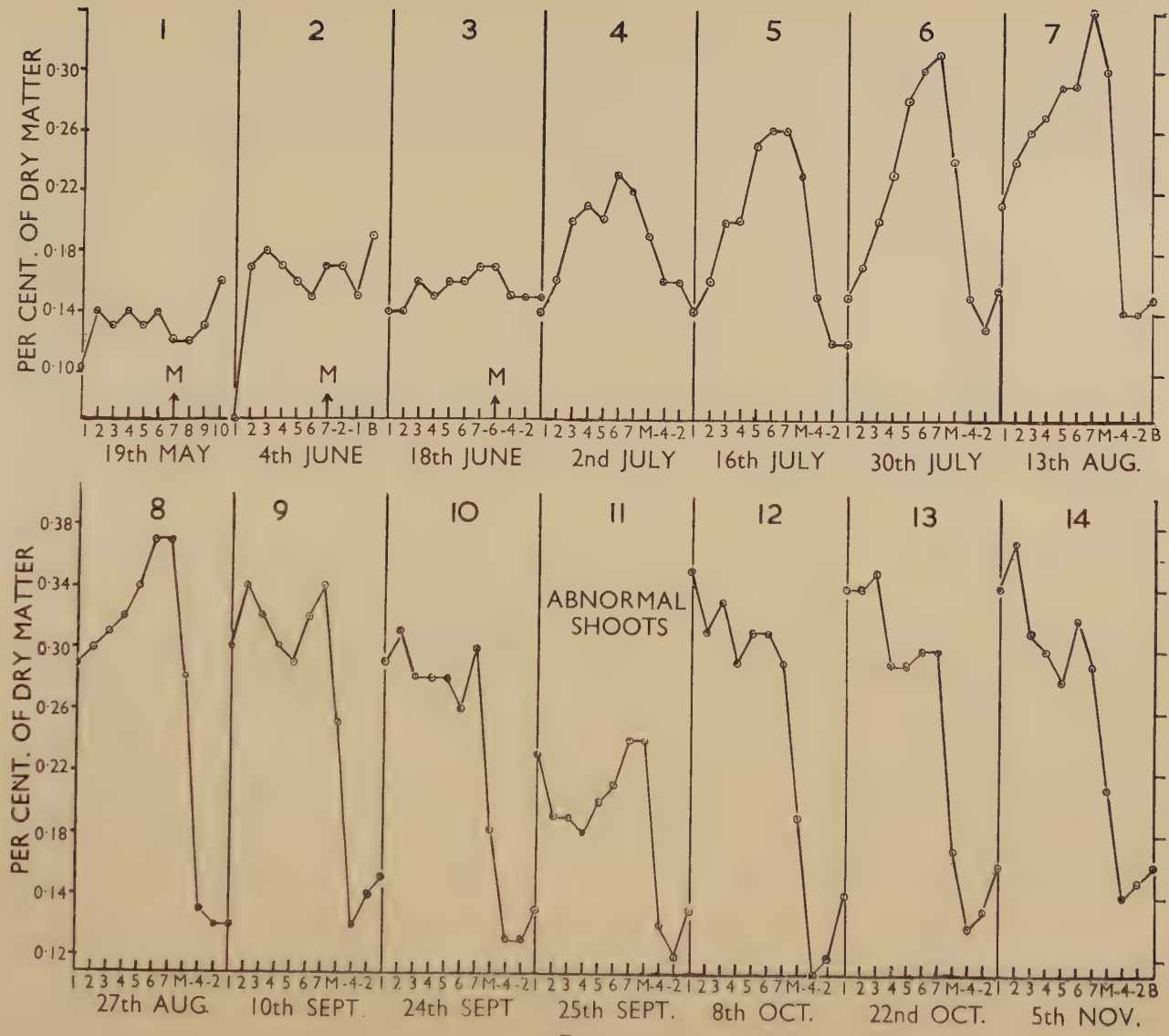

FIG. 5.

MAGNESIUM. See legend under Fig. 1.

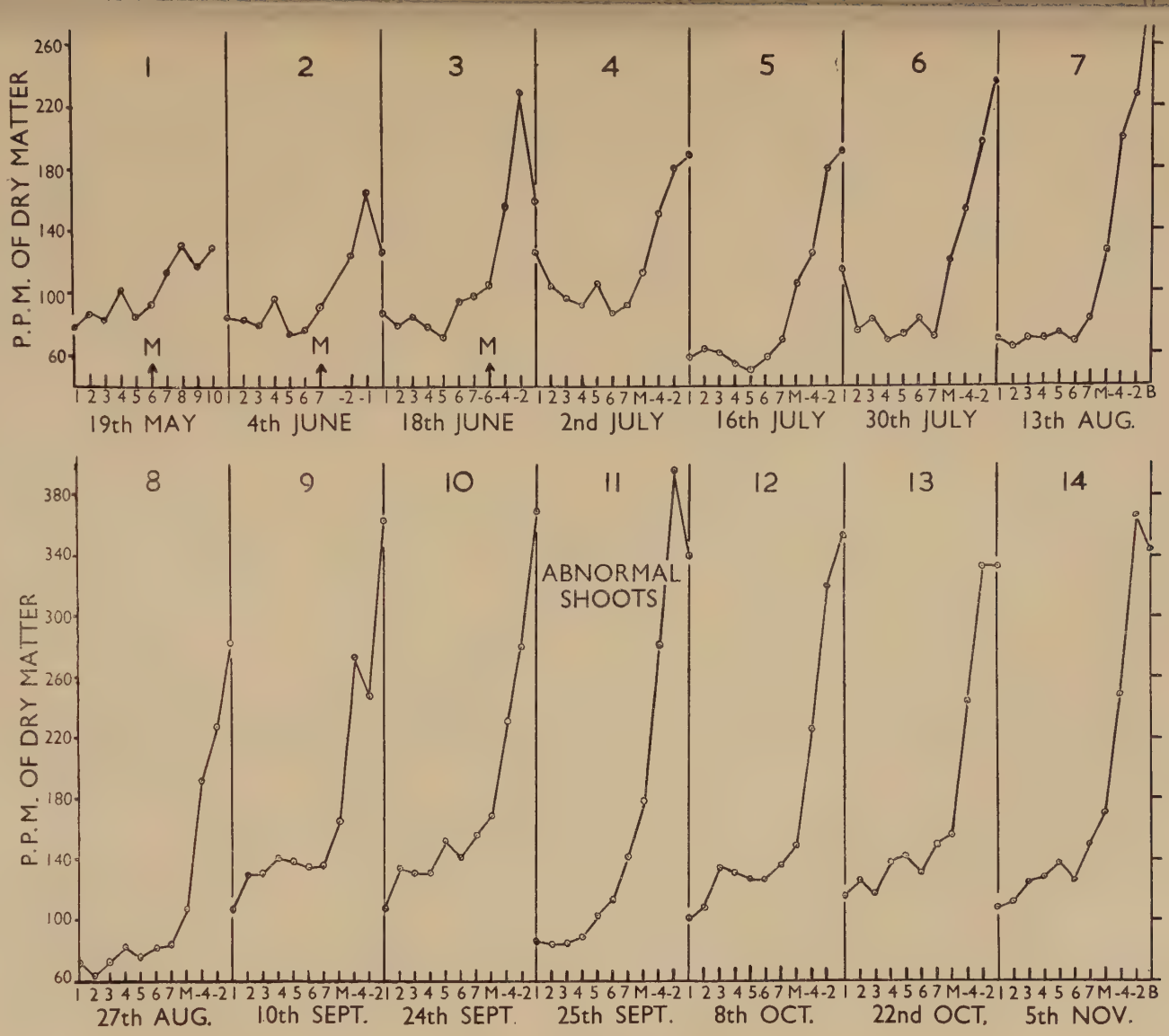

FIG. 6.

IRON. See legend under Fig. 1.

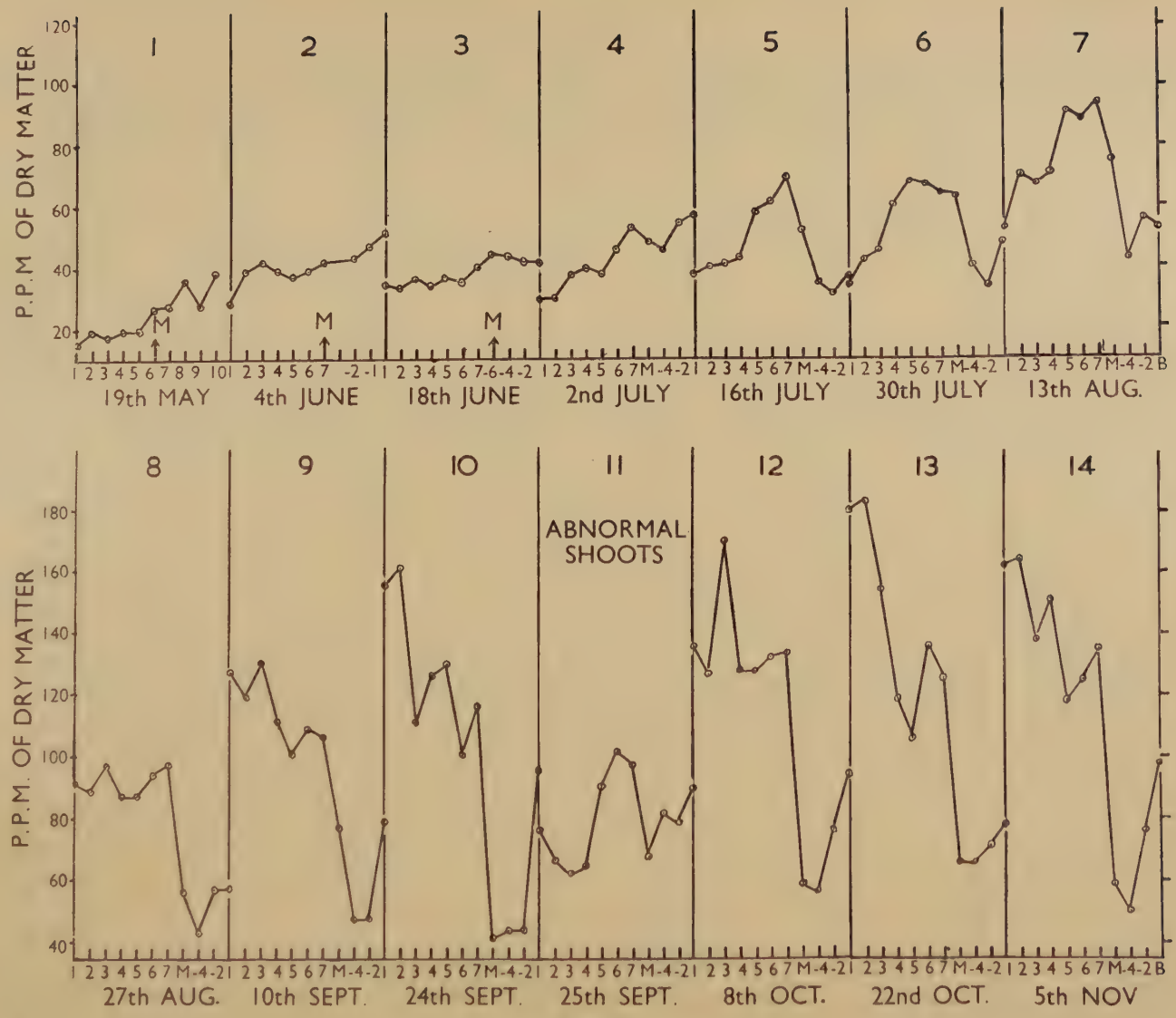

FIG. 7.

MANGANESE. See legend under Fig. 1.

At any time during the period mid-June to mid-August, when vigorous growth occurs and leaves 1 to 7 represent the transition from the rudimentary to the fully mature state, analyses of these leaves show progressive increases in the concentrations of potassium, calcium, magnesium and manganese whereas the concentrations of nitrogen, phosphorus and iron either decrease or remain unchanged.

The concentrations of magnesium and manganese in leaves near the base of the shoot seem to be settled at an early stage and thereafter they remain fairly constant, but the concentrations of these two elements continue to increase in leaves which develop later.

The above few remarks are intended only to draw attention to certain points of interest, for the author hopes that the essential results of the investigation will be clear from a study of the figures and that the considerable body of data summarized therein will serve as a useful reference for workers engaged on the inorganic analysis of leaves. Diagnosis of mineral deficiency by means of leaf analysis is frequently made by comparing the composition of leaves from the unthrifty tree with those from flourishing trees ; indeed, attempts have been made to lay down normal or standard leaf composition values derived from large-scale surveys. The foregoing data emphasize the need for care to ensure that such comparisons are made only between leaves from the same position on the shoot sampled at times when changes in composition occur slowly.

The most suitable leaf position and sampling time are those for which these two factors give rise to the least variation in composition. These conditions are best met for the elements nitrogen, phosphorus, calcium and iron when leaves from the middle of shoots, the M position, are sampled during the middle and latter parts of September (sub-diagrams 9 and 10). Sometimes the youngest fully expanded leaf is sampled during the period of active growth ; in this experiment it corresponds to leaf No. 6 in sub-diagrams 4, 5 and 6, which is apparently satisfactory for nitrogen, phosphorus, calcium, iron and manganese. It is difficult to decide from the diagrams which leaf position and sampling time should be used for the two elements potassium and magnesium but leaves taken from near the base (say the —4 position) in late July would probably give the best data. The leaf positions and sampling times indicated in this work are recommended as those likely to give the least error in making general comparisons of leaf analysis data from different sources ; they are not necessarily those which show the biggest differences in composition due to specific treatments.

SUMMARY.

1. The concentrations of seven elements (N, P, K, Ca, Mg, Fe and Mn) in successive leaves on shoots of apple rootstocks growing in a stoolbed have been determined at fortnightly intervals from May to November.

2. The results here reported are considered to be transferable to vigorous shoots of fruit trees and to give a general indication of the variation in distribution of these elements in the latter, with respect both to position within the shoot and to the date of sampling.

3. The orderly and smooth progression in the distribution pattern with the advancing season may be noted.

4. Considerable variation can occur in the concentration level for specific leaf

positions over so short a period as 14 days, some leaf positions varying less than others.

5. Apical growth is associated with high concentrations of phosphorus and low concentrations of calcium and manganese in the expanding leaves as compared with mature apical leaves on shoots which have ceased growing.

ACKNOWLEDGMENTS.

The author gratefully acknowledges the help in sampling and chemical analysis given by Mr. E. C. Wills, Mrs. B. M. Showler and Mrs. M. Souter.

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(*Received* 12/7/57.)

BOOK REVIEWS

FUNDAMENTALS OF HORTICULTURE. By J. B. Edmond, A. M. Musser and F. S. Andrews. (London and New York: McGraw-Hill Book Co. 1957. Pp. 456, illus. Price £2 10s. 6d., or $6·75.)

Horticulture is concerned with the plant and its environment, with particular reference to the genetics and physiology of a wide range of plant species and the simultaneous control of a number of different attributes of the plant environment. Knowledge in these fields has been accumulating rapidly in the last few decades, and it is doubtful whether the " fundamentals " of horticulture can now be adequately dealt with in a single volume. The danger is that basic plant and soil processes are over-simplified, to the point at which they become incorrect in the light of modern knowledge, yet are still largely unintelligible to students who lack some previous knowledge of chemistry, physics and botany. This second edition of a text-book written primarily for students in the United States fails gallantly in an attempt to cover too wide a field.

Two specific examples may be cited of ways in which the text might be misleading to those with a limited knowledge of the basic sciences. In discussing the effect of atmospheric humidity no mention is made of vapour pressure and references to relative humidity (e.g. p. 57) tend to confuse rather than clarify the situation, whilst the effects of drought on induction of flowering appear to be rather over-emphasized, leading to generalizations which are dangerous in the light of present knowledge of the effects of other factors of the environment on the transition from the vegetative to the flowering condition.

Rather surprisingly, the sections on horticultural practices make no references to mist propagation, the use of plastic films for crop protection and several other new developments which have been widely accepted into American practice. Some of the illustrations are of considerable interest but most are culled from other sources and the line diagrams, notably those in connection with pruning, are not particularly helpful. A more serious criticism is that rather few references are given and only one is dated in the last ten years. There is still a dearth of good text-books on the applications of the main scientific disciplines to horticulture but it seems a pity to refer students to publications twenty or thirty years old when many important aspects of plant physiology and soil science have been excellently reviewed in the scientific journals in the last ten years.

One of the difficulties experienced by students who approach a book of this sort is to decide which statements are founded on scientific work, which are opinions or speculations, and which are descriptions of current empirical practices which may or may not have been the subject of critical study. This book does not always make these distinctions clear.

This is probably the best general text-book on horticulture in print at present and no doubt serves a useful purpose in certain levels of teaching in the United States. However, its usefulness in this country seems likely to be limited, which is a

pity, for there is a sore need for good text-books written to meet the requirements of British horticultural students.

J.P.H.

PLANT PATHOLOGY. By JOHN CHARLES WALKER. 2nd Edition. (New York and London: McGraw-Hill Publishing Co. 1957. Pp. xii+707, illus. Price 75s.)

In this new edition, Dr. J. C. Walker's well-known text-book has been revised and brought up to date with the addition of references to recent publications. The book is well illustrated and retains its characteristic balanced presentation of the field.

The first two chapters, on basic concepts and history, introduce the beginner to the science and practice of plant pathology. The main part of the book is taken up with a fairly detailed treatment of a number of diseases, arranged according to the systematic position of the "incitant", and chosen for their importance in North American agriculture and for their suitability for illustrating general principles. Workers in other areas will inevitably wish that some different diseases had been chosen. For instance, some would value treatment of the diseases caused by *Ophiobolus graminis* and *Cercosporella herpotrichoides* on wheat, *Puccinia polysora* on maize, *Piricularia* and *Helminthosporium* on rice, leaf roll virus of potato and swollen shoot virus of cacao. However, it is unreasonable to expect any one work completely to satisfy the text-book needs of plant pathologists the world over. Dr. Walker has displayed general principles with the diseases he has selected while avoiding the danger of becoming encyclopaedic. I doubt whether the tabulation of synonyms (many of them archaic) of the pathogens is justified in an elementary text-book, and would rather see the space used to develop precise ideas on the dispersal of pathogens in relation to the application of control measures, or to give a fuller treatment of methods of assessing loss from disease.

The last five chapters deal with general aspects of plant pathology, including the influence of the environment and methods of control. Here, in discussing disease control by protective chemicals or by plant breeding, Dr. Walker's well balanced appraisals of current trends are particularly welcome.

The book is not intended as a compendium for the specialist interested in one crop or one kind of pathogen. It is an excellent introduction for the serious student of plant pathology.

P.H.G.

BIOLOGICAL ASPECTS OF THE TRANSMISSION OF DISEASES. Edited by C. HORTON SMITH for the Institute of Biology. (London: Oliver and Boyd. 1957. Pp. 184, illus. Price 21s.)

This volume preserves in permanent format the "raw material" of an outstandingly successful two-day symposium on the general subject indicated by the title, organized by the Institute of Biology and held in London in 1955.

The twenty-two pre-circulated opening contributions by leading research scientists in plant, animal and human pathology, and in the related pure sciences, are reproduced in the order in which they were introduced in the symposium, and

form a sequence in primary emphasis ranging from passive transmission to active transmission, i.e. mediated by another organism, both direct and cyclical, and concluding with special aspects of the subject, such as a survey of the dissemination of plant diseases and pests by human agency and of measures to control it. A list of references to the literature of the particular aspect of the subject dealt with is appended to each of these contributions.

The volume concludes with a record of the principal points and queries raised in the ensuing discussion, under each sub-title, and with useful author and subject indexes.

The merit of this work, as of the event it represents, is that it brings together and discusses within one cover the contributions of representative research workers in the most varied biological fields to a common topic of great interest.

R.V.H.

THE MULCHING OF VEGETABLES. By PATRICIA ROWE-DUTTON. Technical Communication No. 24, Commonwealth Bureau of Horticulture and Plantation Crops. (Farnham Royal : Commonwealth Agricultural Bureaux. 1957. Pp. XIII+165, illus. Price 20s.)

There are many occasions when the horticulturist, whether scientist or market gardener, wants a quick answer to some question concerning mulches and mulching. Would mulching solve this soil problem, ease that cropping difficulty, reduce the weed nuisance, hasten the ripening of this cucurbit or cheapen the harvesting of those sweet peppers, are examples of such questions. Other questions may concern the availability of an easily accessible organic or industrial waste like, for instance, sawdust or corn bagasse. What are its merits, what could it be used on to best advantage, how would it affect the soil, favourably or unfavourably, what are its physical drawbacks, would it persist and clog machines, would it be contaminated with pernicious weeds, might it prove phytotoxic to some crop plants and, above all, what would it cost ?

In Miss Rowe-Dutton's admirable summary of the present knowledge of the mulching of vegetable crops, all these questions are dealt with, and many other aspects of this important subject. But she has done much more than give a summary; the skilful way in which she has assembled and presented the matter makes the book interesting to read and moreover stimulates the reader to wish to know much more of particular materials, their uses and effects.

One of the most discussed subjects at the present time in Great Britain and in the U.S.A. is that of weed control in market garden crops. Chemical methods are often hampered by the undue persistence of the toxicants used or by the risk of taint. Weed suppression, disease control, crop improvement and activity of soil fauna may all be affected by choice of materials for mulching and the timing of their employment, while local weather conditions may fundamentally influence the final result or the balance sheet.

How far can the vegetable grower go with, for instance, a system of straw mulching so successfully used by some fruit growers ? What supplementary manuring programme would be necessary to compensate for the seasonal deficiency of nitrogen ; how far would seasonal excess of soil moisture hold up maturation or delay ripening ? Up-to-date information is here available and the reference list of

upwards of three hundred papers means that the reader can follow up particular lines in even more detail should he so desire. The practices described and the materials listed are of world-wide interest so the usefulness of the publication will be immediately apparent.

The author is to be congratulated not only on her industry but on the wisdom of confining her attention to the mulching of the vegetable crop. The preface states that if sufficient interest is shown in this volume others may follow on the mulching of fruit crops, of tropical crops and of ornamental plants. If such volumes approach the present one in content and style their success is already assured.

H.W.M.

BOTANY. AN INTRODUCTION TO PLANT SCIENCE. By W. W. Robbins, T. Elliot Weier and C. Ralph Stocking. 2nd Edition. (New York : John Wiley & Sons, Inc. ; London : Chapman & Hall. 1957. Pp. 578, illus. Price 56s.)

The first edition of this book, which appeared in 1950, was reviewed at length in this Journal by the late Dr. H. Wormald (Volume 26, p. 246). In the present edition, prepared without the guiding hand of the late Dr. W. W. Robbins, Chairman of the Department of Botany at the University of California, Davis, the authors have endeavoured to keep all changes in line with his concepts of teaching.

Like the first edition, the second, which has been revised and in many parts rewritten, has the student in mind. Substantially, it is the same book, perhaps with more emphasis on plant physiology, that has become a standard text-book in American universities where the science of Botany is taught. The set-up of the book is admirable and there are many new illustrations.

Seven years ago, our reviewer lamented the high price in this country. Alas ! The new edition is even more costly, though perhaps less so than some text-books ; we can only hope that the book, if it is within the means only of botanical libraries, will nevertheless be readily available to the students for whom it has been written.

T.N.H.

CLIMBING AND TRAILING PLANTS. By S. A. Pearce. (London : W. H. & L. Collingridge ; New York : Transatlantic Arts Inc. 1957. Pp. 142, illus. Price 25s.)

Mr. S. A. Pearce, who has had many years of experience in various departments of the Royal Botanic Gardens at Kew, has given us an extremely interesting work of reference in this recent book. He interprets his title widely to include many plants which are not climbers in the botanical sense of the word but can be grown successfully only in the shelter or with the support of a wall ; likewise, he mentions many plants which do not trail but are valuable as ground cover and will tolerate shade. In addition to the sound general information given, there is much to interest the enthusiastic plantsman who wishes to gain further knowledge of many plants which are not commonly grown. The book is a valuable companion to W. H. Bean's " Wall Plants ".

The first half of the book contains much sensible and helpful information which can be applied to the selection and care of all permanent plants. The detailed

cultural instructions given are well known to the old school of practical gardeners who have spent many years in training, but the present generation, who have to acquire their knowledge in a shorter time, will do well to study these pages closely. In them can be found much of the lore which leads to success. A few chapters consist chiefly of lists of plants and recommendations of those which are suitable for various places and various aspects. This part of the book is adequately indexed.

The second half contains detailed descriptions of these plants in alphabetical order, and although Mr. Pearce admits that he does not mention every plant which could be included under the title of the book, one is amazed at the tremendous number referred to.

On the whole the photographs, which, apart from the frontispiece, are not in colour, are good and give clear pictures. In addition, line drawings illustrate various garden operations. One photograph appears to be labelled incorrectly. The Jasminum shown opposite to page 80 has the paniculate inflorescence of *Jasminum polyanthemum* which is a far more tender plant than *J. primulinum*. Apart from this slight error, the book contains much valuable information and can be warmly recommended both to the connoisseur and to the student who wishes to extend his knowledge of uncommon plants.

M.P.

BEEKEEPING. Ministry of Agriculture Bulletin No. 9. (9th Edition.) (London : H.M. Stationery Office. 1957. Pp. 27. Price 2s.)

In these days of expensive text-books, the bulletins of the Ministry of Agriculture, written as they are by experts in their particular fields, are of immense value. This bulletin, first produced in 1922 and now in its ninth edition, is no exception, being written by Dr. Colin Butler of Rothamsted to whom beekeepers will need no introduction. It gives an account written in simple language of all the essentials for success in this ancient and fascinating craft.

T.N.H.

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1. All **manuscripts** should be in double-spaced typewriting, with a good margin, and should be addressed to the Editor, East Malling Research Station, near Maidstone, Kent, England. Papers must be written concisely. Historical reviews should be as short as possible and only such references to literature as bear directly on the subject should be included. Tables and illustrations, if any, must be only such as are absolutely essential for clear presentation.

2. Authors of papers containing extensive **numerical observations** should consult the recommendations of the British Association Committee on Biological Measurements, 1927, obtainable from Burlington House, London, W.1, price 6d. Arrangements have been made whereby original data too extensive for complete publication may be deposited at the British Museum (Natural History), London, S.W.7, or with the Royal Society of Edinburgh, 22 George Street, and thus be available for consultation by other workers. Full bibliographical reference to the publication in which the results are summarized must be supplied with the data.

3. Each paper must conclude with a concise and critically correct **summary** of its actual content. It should contain any new or verified constants as well as any other critical data of permanent value but not tables or graphs. Any organism mentioned should be given its scientific name.

4. Where a paper is of a highly technical nature it should be preceded by a brief **synopsis,** in which its contents are simply and clearly stated for the benefit of non-technical readers.

5. **References to literature** may be by numbers (in brackets) in the text corresponding to a numbered list at the end of the paper or by the Harvard system (author's name and date of publication). By either method, the papers cited should be listed alphabetically according to authors' names, followed by the date of publication. The title of the paper should next be given in full, followed by contracted, but strictly intelligible, title of source of publication, the volume and page numbers. Authors are responsible for the accuracy of their lists of references and should check them carefully in both typescript and proof.

6. The **scientific names** given in the "List of Common British Plant Diseases", published by the British Mycological Society (Cambridge University Press, 1944, revised edition in the press) and "Common Names of British Insect and other Pests", published for the Association of Applied Biologists (1947 and 1952) must be employed.

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10. The suggested **abbreviation** for the title of this publication is *J. hort. Sci.*

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